The flowering behavior of some Trinidad plants

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SINCE hummingbirds feed mainly on nectar, their distribution and abundance must bear some relation to the distribution and abundance of the plants at which they feed. Moreover, the flowering behaviour of the plants must influence the hummingbirds in some way. It was with the object of learning something about this interaction that this study was begun. As the work progressed, this aspect began to recede into the background and an understanding of flowering behaviour as an important part of each plant's life history came increasingly to the fore. In other words, the emphasis began to shift from the birds to the plants.

This preliminary study has produced information that can be followed up in both directions, towards a fuller understanding of the flowering behaviour of some Trinidad plants, together with some others at which I had observed hummingbirds feeding at least once. Plants were listed down the left-hand margin of sheets of paper and the dates and places of observation were recorded along the top. Flowering behaviour was recorded opposite each plant on a simple scale in which a negative sign indicated no flowering and one to three plus signs indicated different degrees of flowering from slight to abundant. A zero sign was used to indicate that the plant had not been seen at that particular time and place. Observations were made on the monthly field trips of the club, on other occasions as opportunity presented and also on short trips made expressly for the purpose of the survey. Most of the sites were in the Northern Range. The period of observation was from January 1976 to December 1978 and from June 1979 to May 1980.

Difficulties in scoring soon became evident. Where plants were clustered together (e.g. *Heliconia psittacorum*) the score tended to represent the number of flowering plants as a proportion of the total; where plants were encountered singly and only a few were seen on any one trip the scoring tended to reflect the extent of flowering per plant as well. No attempt was made to mark individual plants and to count flowers on them as this would have required far more time than was available for the project. Thus, the method is to a considerable extent subjective.

The results for the four years of observation were summarized on histograms. In constructing the histograms, if observations had been made on any one species more than once in any one month the highest level of flowering for that month was recorded. Thus, for the four years of the study the highest score that could be attained for any one month would be twelve plus signs i.e. $4 \times 3$.

*See Appendix for common names.

Nomenclature follows the Flora of Trinidad and Tobago although the names of some of the plants have been changed since publication. It differs from the nomenclature used by Snow and Snow (1972) as follows:

<table>
<thead>
<tr>
<th>Name used by</th>
<th>Name used here</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snow &amp; Snow</td>
<td></td>
</tr>
<tr>
<td>a) Change in specific epithet</td>
<td></td>
</tr>
<tr>
<td>Heliconia bihai</td>
<td>H. wagneriana</td>
</tr>
<tr>
<td>Costus spiralis</td>
<td>C. cylindricus</td>
</tr>
<tr>
<td>Erythrina</td>
<td></td>
</tr>
<tr>
<td>corallodendrum</td>
<td></td>
</tr>
<tr>
<td>Cephaelis muscosa</td>
<td>C. tomentosa</td>
</tr>
<tr>
<td>b) Specific epithet determined</td>
<td></td>
</tr>
<tr>
<td>Justicia sp.</td>
<td>J. secunda</td>
</tr>
<tr>
<td>Heliconia sp.</td>
<td>H. aff. tortuosa</td>
</tr>
<tr>
<td>Costus sp.</td>
<td>C. niveo-purpureus</td>
</tr>
</tbody>
</table>

The plant called *Cephaelis muscosa* by the Snows is stated to have red flowers and since *C. muscosa* has white flowers it is clearly mis-identified. I assume the correct identification to be *C. tomentosa* which has yellow flowers in a compact head subtended by two scarlet bracts. The complete identification of the partly identified plants is based principally on the fact that these three are all known to be common in the Arima Valley where the Snows worked.

RESULTS

At the start of the survey I did not know all the plants in the Snow's list but I optimistically thought I could get to know them. This hope was not realized for some I never saw and others I learned to recognize too late to be of value. Thus, several plants (including all the bromeliads) were eliminated from the survey. Other plants that I knew well were seen too infrequently for the records to be meaningful. Thus, the report is concerned with a total of 38 plants for which adequate records were obtained.

After one year it was apparent that some plants were always in flower and recording of their behaviour was discontinued then or after one further year. Though no systematic recording of their behaviour was continued, further casual observations support the original assessment of continuous flowering at a fairly constant level. Six plants are on this list: *Listantianthus cheholoioides*, *Stachyotapheta jamaicensis*, *Asclepias curassavica*, *Lantana camara*, *Cordia curassavica* and *Isotoma longiflora*. The last-named, included in the study on the strength of one visit by the Copper-rumped Hummingbird, is probably not
FIG. 1. PLANTS that flowered year-round.

FIG. 2. FLOWERING patterns of plants that flowered seasonally.

FIG. 3. FLOWERING behaviour of the plants that flowered neither seasonally nor year-round.

FIG. 4. FLOWERING behaviour of all the plants combined.
a flower that is used as a nectar source by hummingbirds since the corolla is much longer than the bill of even a large hummingbird. It appears to be a moth-pollinated flower.

After the data for the four years had been plotted other plants were revealed as flowering the year round. These plants are Heliconia wagneriana, H. hirsuta, H. psittacorum, Centropogon surinamensis, Cephalis tomentosa, Duggea hirsuta and Palicourea crocea. For the three species of Heliconia there is a suggestion that flowering is more abundant in the wet season than in the dry but for the others there is no indication of a season for increased flowering.

All the other results are shown in Figures 1 - 3. Of the plants in Fig. 1, four flowered for all except one month of the year. Three of them, Mandevilla hirsuta, Hamelia erecta and Isertia parviflora were not seen in the relevant month in any of the four years and the fourth, Psychotria uliginosa, was seen once not in flower. Thus, all of these are regarded as plants that flower year-round for which records are simply lacking for one month. The other plants in the figure (Heliconia aff. tortuosa, Costus cylindricus and Tussacia pulchella) also were not seen in the months for which no flowering is recorded and because the months with no records are not contiguous as though representing a definite season with no flowers, these plants too are regarded as flowering year-round.

The plants in Fig. 2 are different for they give clear evidence of seasonal flowering. Most of them flower in the dry season; the exception is the chaconia, Warszewiczia cocinea, which flowers mainly in the wet season. From Fig. 2 it may seem that W. cocinea is a plant that flowers the year-round with observations missing for two months; but this is not the case. Flowering begins with the showers of April or May, increases to a maximum in the months June to August and thereafter declines. There is a complete absence of flowering in the driest months, February and March. All the other plants of Fig. 2 flower in the dry season with perhaps some carry-over into the wet. They are Pachystachys cocinea, Ipomoea tilicaea, Combretum fruticosum, Norantea guianensis, Erythrina pallida, Brownea latifolia, Cordia alliodora.

The plants of Fig. 3 do not fall neatly into any of the previous categories. From the data in the figure, Psychotria innundata would seem to be a plant that flowers the year-round with observations lacking for one month. In fact, its behaviour is quite different. It flowers in short bursts of three or four weeks' duration. There is then a period of some months without flowering after which there is another short period of flowering. The cycles are not regular from year to year nor are they absolutely synchronized in all localities so that over the four-year period flowering has been observed in most months of the year, giving the impression of year-round flowering. The second plant in Fig. 3, Acnistus arborescens is similar except that its cycles of flowering seem to be restricted to the dry season.

The remaining plants of Fig. 3 all show many months of flowering but more observations are required to determine the true nature of their flowering behaviour. Costus niveo-purpureus may flower the year round as does C. cylindricus, or it may stop flowering in the dry season or, possibly, do one or the other depending on locality. Justicia secunda and Dioclea guianensis probably flower the year round. Apheleaandra incerta may have a period of purely vegetative growth in the wet season but has been observed in flower in the Central Range in September and October 1980 so this possibility is now less likely than year-long flowering. Symphonia globulifera probably flowers throughout the year. Before this study was begun one particular tree was observed repeatedly every month for a year and was in flower every month but May. Rudgea freemani at Leotaud Trace, Talparo flowered only in the early wet season in 1979 and 1980 but, as the data show, plants elsewhere have not been so restricted. Two individuals of Calliandra guildingii were in full flower in September 1980 whereas the picture of seasonal flowering presented in Fig. 3. It may have a cyclic flowering pattern rather than a seasonal one. There is nothing to add to the data in Fig. 3 on Vismia cayennensis.

**DISCUSSION**

**The methods**

It is obvious that the methods used are not those that would be used by a professional biologist working full time on the project. The methods were devised to suit the conditions under which the work had to be done and can be expected at best to give no more than a preliminary indication of the flowering behaviour of each plant. If all the data had been gathered over a period of only one year then cyclic flowering and seasonal effects would have been much more obvious. The flowering period of W. cocinea, for instance, would probably have been shorter by several months but in my survey with different rainfall patterns over the four years the flowering period seems extended by comparison. Croat (1975) makes the same point in relation to his data on flowering on Barro Colorado Island.

A similar effect is produced by spreading the survey over a large area for the onset of rain or drought is not the same everywhere. In this survey Heliconia wagneriana has been revealed as flowering year-round though it is my impression that flowering is heaviest in the early rainy season. At Finca La Selva in Costa Rica the same plant has a distinct flowering period from December to June with a peak in the driest months of February and March and no flowering in the rest of the year (Stiles, 1975). Finca La Selva is at almost the same latitude north of the equator as is Trinidad and the seasons are very similar to those here. Why then do the two populations of plants behave so differently? Is it because of the factors mentioned in the preceding paragraph or are they two distinct species bearing the same name?

**Plants with year-long flowering**

Twenty of the thirty-eight plants have been shown to flower year-round and three or four of those in Fig. 3 probably do as well. Of the twenty, nine are shrubs, ten are herbs and one is a vine. Most of these plants are either weeds or grow in moist, shady places where seasonal changes are not so pronounced and continuous flowering might be expected. The exceptions, Isertia parviflora, Hamelia erecta, Duggea hirsuta, Cephalis tomentosa, Centropogon surinamensis and Heliconia psittacorum, might have been expected to show some seasonal behaviour and further study of these is desirable.

**Seasonal flowering**

The chaconia, W. cocinea, exists in two varieties, the single or wild type and the double which is becoming popular as an ornamental. The latter was propagated from a single wild sport found on the Blanchisseuse Road which has since been cut down so that the double variety no longer exists in the wild (Nichols, 1963). It is interesting that this variety flowers more abundantly and consistently in the dry season than in the wet although the wild type, to which my observations refer, is the only plant in the survey that has a distinct, wet-season flowering period. This may be at least partly the result of the special environmental conditions associated with cultivation. Some other members of its family, the Rubiaceae, seem to follow a pattern of wet season flowering but all the other Rubiaceae in this survey seem to flower year-round except Rudgea freemani for which records are relatively incomplete.

Of the plants in Fig. 2 the seasonal behaviour of most is quite marked and unmistakable even including Pachystachys cocinea and Norantea guianensis with their long flowering spells, which include part of the wet season. But at the time of writing, October 1980, two plants of Brownea latifolia were seen with two flowers each near Machapure Hill in September 1980. More observations on this plant should be rewarding.

**The stimulus of flowering**

For the plants that flower year-round the stimulus for
flowering is probably the attainment of maturity. For those that flower seasonally the stimulus is probably some change in the environment. Changes in water status of the soil or humidity of the atmosphere are the most likely stimuli but changes in temperature and day length cannot be ignored. At first sight it is hard to believe that day length could be important in plants with such long periods of flowering as *Pachystachys*, *Norantea* and *Erythrina* and change in water status would seem to be the stimulus. Yet, beginning of flowering in all coincides with the period of shortest days and suggests that water status is not everything and that day length is important. The short flowering period of *Combretum fruticosum* suggests the over-riding importance of day length and this might be confirmed by further observation. However, experimentation, which is better than simple observation, would be difficult with any of the plants of Fig. 2 except *Pachystachys* and since none of the others is an important crop plant or a particularly popular ornamental they are not likely to attract the attention of professional botanists.

The flowers in relation to hummingbirds

Croat (1975) studied the flowering and fruiting phenology of each of the 1253 species of flowering plant on Barro Colorado Island in the Panama Canal Zone and found that the number of species in flower declined from a peak in March to a trough in November and then rose again. Casual observation suggests that the pattern of flowering in Trinidad is similar and this supposition is supported by the present results. When the scores for all 38 species are pooled and plotted as described earlier (Fig. 4) it is seen that from a peak in January flowering declines to a minimum in November. It should be noted that Barro Colorado is just over 9° north of the equator (as against Trinidad's 10°) and that its rainfall pattern is very similar to that of Trinidad with a dry season from mid-December to May and a rainy season for the rest of the year.

Therefore, hummingbirds must face a relative scarcity of flowers in the late rainy season as against a relative abundance in the dry season. This must surely be the reason why so many of our hummingbirds are migrants, nesting here in the dry season and departing when the rains come. Yet, beginning of flowering in all coincides with the period of shortest days and suggests that water status is not everything and that day length is important. The short flowering period of *Combretum fruticosum* suggests the over-riding importance of day length and this might be confirmed by further observation. However, experimentation, which is better than simple observation, would be difficult with any of the plants of Fig. 2 except *Pachystachys* and since none of the others is an important crop plant or a particularly popular ornamental they are not likely to attract the attention of professional botanists.

The common name and families of the plants

1. *Acnistus arborescens* (Solonaceae) wild tobacco.
2. *Asclepias curassavica* (Asclepiadaceae) milk weed, mantae, wild ipecacuanha.
3. *Brounnea latifolia* (Caesalpiniaceae) cooperhoop, mountain rose.
5. *Centropogon surinamensis* (Campanulaceae) deer meat, crepe coq.
6. *Cephaelis tomentosa* (Rubiaceae) wild ipecacuanha
7. *Cordia alliodora* (Boraginaceae) cypre, cyp.
8. *Cordia curassavica* (Boraginaceae) black sage.
10. *Heliconia psittacorum* (Strelitziaceae) cocoa lily, wild ginger.
11. *Heliconia wagneriana* (Strelitziaceae) balisier.
12. *Isertia parviflora* (Rubiaceae) wild ixtora, bois fer.
16. *Norantea guianensis* (Maregraviaceae) red hot poker, beacon.
18. *Rudgea freemani* (Rubiaceae) bois tatoo, kapakol.
20. *Symphonia globulifera* (Guttiferae) yellow mangue.
22. *Warszewiczia coccinea* (Rubiaceae) chacoon, chaconer, wakamy, wild poineettia.

ACKNOWLEDGMENT

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REFERENCES


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APPENDIX

The three hermits are year-long residents. Calculations from the data of Snow and Snow (1972) reveal that only five plants accounted for 88% of the visits of *Glauca hirsuta* and 76% of *Phaethornis guy*. These plants are *Centropogon surinamensis*, *Pachystachys coccinea*, *Heliconia wagneriana*, *H. hirsuta*, and *Costus cylindricus*. All but *P. coccinea* flower year-round. Of these only *C. surinamensis* is unimportant to *Phaethornis longuemars.* The remaining four with *Cephaelis tomentosa*, *Justicia secunda* and *Palicourea crocea* accounted for 75% of its visits. Of these seven plants only *Justicia* and *Pachystachys* do not flower year-round. Omitting the seasonal plants the remaining ones account for 76%, 61% and 50% of visits by the three hummingbirds. It is clear, therefore, that all the hermit hummingbirds depend heavily on plants that flower continuously.

The remaining hummingbirds in the Snows' list are not so easily dealt with. The records for three ( *Florisuga melivora*, *Anthracothorax nigricollis* and *Chrysolampis mosquitos*) are too few to be meaningful in this context. For the remaining three ( *Chlorostilbon notatus*, *Amauliana chiperitectus* and *Amauliana tobaci*) nine plants account for most of their visits. Two of these plants are not native and two were omitted from this report for lack of sufficient data. The remaining five, *Pachystachys coccinea*, *Palicourea crocea*, *Calliandra guildingii*, *Isertia parviflora* and *Warszewiczia coccinea* account for 27%, 28% and 38% respectively of the visits of these hummingbirds. Here there are only two plants that flower continuously, *P. crocea* and *I. parviflora*, so that these three hummingbirds exploit seasonal flowering more than the hermits do.