



Bee Arrival at Two Costa Rican Female *Catasetum* Orchid Inflorescences, and a Hypothesis on Euglossine Population Structure

Daniel H. Janzen

Oikos, Vol. 36, No. 2. (Mar., 1981), pp. 177-183.

Stable URL:

<http://links.jstor.org/sici?sici=0030-1299%28198103%2936%3A2%3C177%3ABAATCR%3E2.0.CO%3B2-U>

Oikos is currently published by Nordic Society Oikos.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/oikos.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Bee arrival at two Costa Rican female *Catasetum* orchid inflorescences, and a hypothesis on euglossine population structure

Daniel H. Janzen

Janzen, D. H. 1981. Bee arrival at two Costa Rican female *Catasetum* orchid inflorescences, and a hypothesis on euglossine population structure. – *Oikos* 36: 177–183.

Two 5-flowered inflorescences of *Catasetum maculatum*, produced 44 d apart, attracted at least 407 male *Eulaema polychroma* euglossine bees, as well as 5 male *E. cingulata* and 2 *E. meriana* over 59 flower-days and 14 inflorescence-days in the early rainy season. Two bees arrived carrying pollinaria and they pollinated 3 flowers. Of the 144 bees marked at the second flowering, 9 had been marked at the first flowering 44 d earlier. Estimates of the size of the male *E. polychroma* population generating these results range from 931 to 4208. The higher number is probably more reliable. The possibility that these males may be drawn from a large pool and the results of other euglossine bee studies in Costa Rica lead me to hypothesize that, especially in a highly seasonal habitat, the male euglossine bees may range very widely and find nectar, orchids and mates in 3 quite different habitats. Females may find their resources in a geographically more restricted area and their habitat may intersect with those of the males only in courtship areas.

D. H. Janzen, Dept of Biology, Univ. of Pennsylvania, Philadelphia, PA 19104, USA.

Два пятицветковых соцветия *Catasetum maculatum* выращенных за 44 дня отдельно, привлекли по меньшей мере 407 самцов пчел *Eulaema polychroma* а также 5 самцов *E. cingulata* и 2 – *E. meriana* в течение 59 цветко-дней и 14 соцветие-дней, в начале сезона дождей. 2 пчелы имели поллинии и опылили 3 цветка. Из 144 пчел, меченых при вторичном цветении, были помечены и при первом цветении, на 44 дня раньше. Определения численности самцов в популяции *E. polychroma*, давшей эти результаты, колебались в пределах от 931 до 4208. Большие цифры очевидно более достоверны. Возможность извлечения этих самцов из большого рула, и результаты других исследований пчел *Euglossinae* в Коста Рике привели меня к созданию гипотезы о том, что особенно в местообитаниях с большими сезонными различиями условия самцы пчел могут сильно отличаться по величине и находить нектар, орхидные растения и самок в 3-х самых разных типах местообитаний. Самки могут находить свои ресурсы в более ограниченных географических районах, и их местообитания могут пересекаться с местообитаниями самцов на участках брачных игр.

Accepted 10 June 1980

© OIKOS 0030-1299/81/020177-07 \$ 02-50/0

Introduction

It is well known that *Catasetum* flowers are pollinated by male euglossine orchid bees (Crüger 1865, Darwin 1877, Dodson 1962, Pijl and Dodson 1966). The bees remove several chemicals from *Catasetum* (and other orchid) flowers with brushes on their front feet, transfer the chemicals to special grooves in their hind tibiae, and use them for unknown purposes in their own physiology (Dodson et al. 1969). Degradation products of the chemicals appear in mandibular gland secretions (N. H. Williams pers. comm.) but the secretions are of unknown function. Just as with other orchids pollinated by euglossine orchid-bees no one has examined the quantities of bees that visit *Catasetum* inflorescences in a natural habitat (see Williams 1978 for a thorough bibliography of orchid-bee papers). Here I describe the visitors and pollinators at two sequential 5-flowered female inflorescences on one *Catasetum maculatum* orchid.

The plant

A large healthy adult *Catasetum maculatum* was found near the north end of Playa Naranjo in Santa Rosa National Park (SRNP), which is in deciduous forest on the Pacific coastal plain of Costa Rica (Guanacaste Province) near the Nicaraguan border. The plant was transplanted to a large horizontal branch 2 m above the ground in a *Guazuma ulmifolia* tree in front of the most southwestern building ("bodega") of the SRNP administration area in July 1978 (mid-rainy season). Here it was exposed to broken sunlight as the sun moved across the irregular *Guazuma* crown. Between March and May 1979 it produced its first inflorescence at this location, and its unpollinated flowers attracted bees from 21 through 28 May. A second inflorescence began to appear immediately after and flowered 10–15 July; three flowers on this inflorescence were pollinated by bees.

The site is approximately 10 m from the edge of early to late secondary succession woody vegetation mixed with old ungrazed pastures of various sizes. This vegetation contains nectar and pollen hosts for euglossine orchid bees at certain but not all times of year. *C. maculatum* is a rare plant in SRNP and the closest free-living plant is approximately 150 m north on the side of an *Acrocomia* palm. The only other known individual in SRNP is growing at the site where the transplant was found (about 10 km west) on the ground on a tangle of rocks and branches.

The inflorescences

There were five female flowers on each of the yellow-green inflorescences, and each flower faced away from

the central axis so as to produce approximately equal numbers of degrees between each of the 5 lines of approach. The buds of the first inflorescence began to open on 15 May 1979, the first odors were produced by the most proximal flower on 18 May, and the five open unpollinated flowers ceased odor production after the morning of 27 May. The buds of the second inflorescence did the same; the most proximal was the first flower to attract bees (10 July). The last day of attraction was 15 July, and the pollinated flowers stopped producing odor on the day of pollination.

No rain fell from 21 through 28 May, though the rainy season had begun on 25 April. The weather was sunny and breezy. During 10–15 July no rain fell in the morning but there was afternoon rain and extensive cloudiness during the day and evening. During the dry season at SRNP, *C. maculatum* is leafless and does not bear flowers.

The visitors

Bees began to arrive at the inflorescences 15–30 min before the sun rose above the forested horizon at about 0600 hours. The arrival rate began to taper off about 3 h later and the last bee usually arrived about 0930 hours. They flew up to the inflorescence, hovered in front of one or more flowers, landed, crawled into the inverted cup, stayed for as much as 10 min if undisturbed, and dropped out and flew away or entered a second flower. This sequence was often broken when bees backed out of the flower to hover in the air, apparently transferring material from the front to the hind legs as described by other authors (Evoy and Jones 1971, Michener et al. 1978). However, such hovering often resulted in pre-emption of the flower by another bee. If there was a bee in a flower when another arrived (a very common case), the newcomer attacked the rear end of the occupant with mandibles and feet. If the attack was intense, the occupant sometimes backed out and was replaced by the aggressor, or they grappled and both fell away, with yet a third bee then sometimes occupying the flower. I saw a maximum of 18 bees at an inflorescence at one time and almost always there were 2–8 present.

Three species of *Eulaema* (all males) were the only bees that arrived at the inflorescence. All but a few arrivals were *E. polychroma* (= *E. tropica* of older literature) and only this species is discussed below. *Eulaema meriana* came twice, but did not even attempt to enter a flower (though it is not too large to do so). An *Eulaema cingulata* was taken from inside a flower on 23 May, marked and released. Two other *E. cingulata* were observed to enter the flowers on 24 May and behave just as did the *Eulaema polychroma* males. Two more came on 11 July.

A total of 407 male *E. polychroma* bees were marked at the two inflorescences (Tab. 1). Each was caught by

Tab. 1. Male *Eulaema polychroma* arrivals at two successive 5-flowered inflorescences of a *Catasetum maculatum* orchid.

<i>First flowering</i>	May	21	22	23	24	25	26	27	28	
No. of odoriferous flowers		1	5	5	5	5	5	5	0	
No. of bees marked		5	56	57	62	28	18	36	1	= 263
No. of bees recaptured from	May	21	22	23	24	25	26	27	28	
		0	0	0	0	0	0	0	0	
			5	0	3	0	0	2	0	
				5	6	1	0	1	0	
					1	1	0	3	0	
						0	0	0	0	
							0	0	0	
								0	0	
									0	
Estimated population size					931	2700		1582		
<i>Second flowering</i>	July	10	11	12	13	14	15			
No. of odoriferous flowers		1	5	5	3	2	2			
No. of bees marked		6	35	45	29	27	2			= 144
No. of bees recaptured from	July	10	11	12	13	14	15			
		0	0	0	0	0	0			
			0	0	1	0	0			
				3	2	3	0			
					0	0	0			
						0	0			
							0			
Estimated population size					1333	1150				
Number of bees recaptured from 21–28 May		1	3	2	3	0	0			= 9
Estimated population size										4208

hand by pinching or poking the bee in the cup and grasping the bee with the fingertips as it emerged backwards. The bee was held in one hand for a few seconds while a small patch of the yellow abdominal hairs was shaved off carefully with a razor blade. The abdominal tergites are black and the bee was therefore conspicu-

ously and permanently marked (bee hairs do not grow back). On 21 and 22 May the bees were marked individually. They were marked differently in daily batches on each of later days. When I put my hand up to the inflorescences, there were often 1–3 bees in the flowers and 1–5 hovering around the inflorescences. In captur-

Fig. 1. Five flowers of *Catasetum maculatum* being visited by 12 male *Eulaema polychroma* bees. In the lower center, the two blurred bees are fighting in the air, after one has pulled the other out of the flower. In the upper center, a male bee has just landed on the back of an earlier arrival in an attempt to pull him away from the flower (Santa Rosa National Park, Guanacaste Province, Costa Rica).



ing those in the flowers, I usually frightened off about a third of the hovering bees. However, many of these were observed to circle widely and return directly to an inflorescence. Once a bee had been handled, it usually left. For example, only 5 of the 56 bees marked on 22 May returned to enter a flower that morning (though 2 of these returned twice). No bee was recaptured on more than one day (recaptured bees were further individually marked).

The minimum estimate of the number of bees arriving at the two inflorescences is 407. It is my impression that about 100 more came to the first inflorescence and 50 more came to the second. However, I will treat the sample of 407 as the actual arrival number for calculation purposes. The bees ranged in condition (and therefore age) from specimens with perfect wing margins and bright yellow abdomens to very badly frayed wing margins and abdomens faded to almost white.

No bees of any species arriving at the first inflorescence bore pollinaria; two *E. polychroma* had the base of a viscidium firmly attached to the dorsum of their thorax or upper abdomen. None of the five flowers received a pollinium and all wilted severely by 29 May. The second inflorescence attracted two bees that bore one pollinarium each. One bee pollinated two flowers on July 12 and the other pollinated one on July 13.

Results and discussion

This orchid obtained at least 407 trials at pollination by *E. polychroma* with 59 flower-days and 14 inflorescence-days over 56 d in the first third of the rainy season. This produced three pollinated flowers from one or two parents. Less carefully recorded observations at other *Catasetum* orchids and at artificial baits in this and other Costa Rican habitats suggest that the paucity of pollinaria on the 407 *E. polychroma* is representative of the usual state of pollinator quality for euglossine bees (Janzen et al. 1980) (though in Panama a somewhat greater number of euglossines arrive at chemical baits bearing pollinaria (J. D. Ackerman pers. comm., N. H. Williams pers. comm.)).

Two different types of estimate are available for the size of the pool of bees from which the bees were drawn (the area of influence of the orchid). There are three days in the first flowering and two in the second when a known number of bees that had been marked on immediately previous marking days were circulating and some of these were recaptured. By dividing the number of captured bees by the number available to catch for each of these days, I estimated that the bee pool was 931 to 2700 bees (Tab. 1) with an average of 1539 ($m = 5$, $s.d. = 692$). Additionally, bees marked in the first flowering were recaptured during the second flowering. By the same method, I calculated that the bee population being drawn from contained at least 4208 bees. Both of these estimates require that there is no

exit or entry to the bee population from the time of marking to the time of recapture, that the probability of recapture is not affected by the previous capture, and that there is a thorough mixing of the marked bees among the unmarked pool. I will discuss each assumption in detail as a way of illuminating the bee-orchid interaction.

Other unpublished studies of *Eulaema* in SRNP and neighboring parts of Guanacaste suggest that the females of this bee provision cells heavily in the dry season (December through April) and that many of the bees produced by these cells have emerged by the beginning of the rainy season. There follows a period of 5–6 months (June–November) when males and females are primarily active as nectar collectors but little pollen collecting occurs. I suspect that most of the male bees attracted to this orchid had hatched during the previous four months and that relatively few were hatching during the time encompassed by the two flowerings I observed. For three reasons I suspect that few died of old age or predation during this period. First, few of the males were worn and faded; most of those that arrived at both inflorescences had deep orange to yellow abdomens (instead of the faded cream color of old bees of this species) and did not have strongly frayed wing-tips (as is commonplace with bees with faded abdominal colors). Second, the nine recaptured individuals marked at the first flowering and recaptured at the second flowering were fresh and unworn in appearance despite their known age of at least six weeks. Third, female euglossines are highly aposematic, robust, and possess a very vicious sting. The males are behavioral and color mimics of the females and I suspect are very rarely taken by predators. I do suspect, however, that many of the marked bees moved outside of the range of the attraction of the orchid and that this is the cause of the decline in the number of bees that were marked in the first flowering which arrived at the second inflorescence (see below).

While generally avoided in discussions of mark and recapture of euglossine bees at artificial chemical baits, it is quite possible that marking directly influences the probability that the bee will return. First, a euglossine bee may be the kind of machine that registers "task completed" once it has arrived at an orchid (since arrival would normally mean that it would get some reward) and once it is then frightened away or leaves because it is satiated, it may not return to the "attractable" state for a fixed period that is longer than the lifespan of the inflorescence. That certain bees returned on the day of marking, or on immediately following days, rules this out as an absolute possibility but does not rule out the chance that the bees are variable for such a trait. Second, capture at an inflorescence may signify that there is a very naive or very smart predator perched by the orchid (such as an experienced insectivorous capuchin monkey) and therefore it ought not to be revisited. Again, the return of marked bees shortly after

they were marked either negates this or suggests a variable population.

That the bees may mix thoroughly with the population between the time of marking and recapture is in the realm of pure speculation. All I can say is that large female euglossine bees fly fast and far when there is a nest to return to (Janzen 1971) and there is no reason to suspect that the males are not equally mobile. In Dresler's (1979) words "the eulaemas are strong-flying insects, with the males apparently rather nomadic".

In short, with respect to the paucity of recaptures of bees marked within the life of an inflorescence, there is no way to distinguish between the possibility that once marked, the bees rejoined and thoroughly mixed with a huge attractable pool and that once marked (having entered the flower), the bees were no longer available for attraction for a while. I favor the later hypothesis because it is consistent with a coevolved natural history that maximizes the chances that the visiting bee is carrying a pollinarium, but I realize that the population estimates (931–2700, Tab. 1) based on recaptures of recently marked bees are then nonsense.

For recaptures in the second flowering, of bees marked in the first flowering, the story is different. It is extremely unlikely that the marked bees remember the site of a single capture for six weeks, and one visit to an orchid is quite unlikely to have satiated the bee for six weeks. Therefore the proportion that arrives may more truly represent the proportion of marked bees in the population (six weeks is probably also enough time for as much mixing as will occur). However, there is no way to know by what area the estimate of 4208 bees should be divided to get a density estimate. These bees could be coming from as far as 10 km and as little as 100 m. My field experiences with euglossines (Janzen 1971 and unpublished) suggests an estimate of kilometers is more reasonable than one of hundreds of meters.

The bee which pollinated two flowers in the second flowering had visited at least three *C. maculatum* inflorescences in 6 wk. It had been marked on 22 May and must have later visited a male inflorescence to pick up the pollinarium.

The species composition of the visitors and the pollinators strongly suggests that *E. polychroma* is the normal pollinator of *C. maculatum* in SRNP (in other parts of Central America, *Catasetum* attracts other euglossine species as well). However, we have taken *Eulaema cingulata* and *E. nigrita* commonly, and *E. meriana* and *E. bombiformis* rarely at chemical baits within 1–3 km of the orchid (Janzen et al. 1980). *E. polychroma* has never been taken in SRNP at the baits used to attract these other four *Eulaema* (methyl cinnamate, benzyl acetate, eugenol, cineole, methyl salicylate). No other species of *Catasetum* or other orchid that is pollinated by euglossine bees is known from SRNP (Janzen and Liesner 1980).

The above observations, speculations and interpretations, coupled with my past experiences with female *E.*

polychroma at nests and flowers, lead me to propose a hypothetical population structure for euglossine bees which is a fairly drastic departure from that conceived for most insects. However, it differs only in scale from that of such insects as those species of butterflies in which males and females usually occupy quite different feeding and displaying microhabitats.

I propose that a male orchid-bee ranges over or uses one habitat for orchids, another for nectar, and yet a third for courting. All three habitats may be many kilometers apart. A female, on the other hand, probably finds pollen hosts, nectar hosts, nests, and males in the same geographic area, if not in the same habitat. I suspect that the separation of male habitats from each other and their distinctness from those of the female is strongest in highly seasonal habitats such as SRNP and weakest (if it occurs at all) in the rainforest habitats. Furthermore, the large *Eulaema*, which are year-round present at chemical baits (Janzen et al. 1980) and have extremely wide geographic ranges, should fit this model most closely while the more seasonal *Eufriesia* and many of the small *Euglossa* should fit it most loosely. The latter two genera are perhaps likely to find, as part of their more specialized life styles more of their resources within one or a few habitats.

Two natural history observations of *Eulaema* and other euglossines in SRNP support, but do not demonstrate, the accuracy of the model proposed above.

(1) I have never seen a female of *Eulaema nigrita*, *E. meriana* or *E. cingulata* in SRNP in five years of field work there in all seasons, yet the males are occasionally taken at nectar hosts and are reliable visitors at chemical baits in all seasons. *Eulaema polychroma* females are common at pollen and nectar hosts in SRNP only during certain seasons.

(2) There is only one species of orchid-bee visited orchid in SRNP but collecting with baits yielded 18 species of euglossines (Janzen et al. 1980). Some of these bees carried pollinaria of species (*Gongora*) that do not occur in the Park but do occur in the evergreen forests beginning at about 600 m elevation and 20 km from the northeast boundary of SRNP. Aside from the *Eulaema* species listed about, only 2 of the 18 other species has been taken at nectar or pollen hosts in the Park (and females of these 2 species are commonly taken at nectar or pollen hosts).

I hypothesize, therefore, that the euglossine bee structure of SRNP is the following. There is one large *Eulaema*, *E. polychroma*, that breeds in the Park and three other species whose males occasionally enter the Park for nectar and would enter the Park for orchids if the right species grew there (as shown by their presence at the chemical baits). *Eulaema polychroma* pollinates the one species of euglossine-pollinated orchid in the Park but this orchid is occasionally visited by *E. cingulata* as a source of chemicals. This bee normally uses the Park for nectar and usually goes elsewhere for orchids and females. A female *E. cingulata* has never

been seen in SRNP. *Eufriesia mexicana* breeds in the Park, but the males go elsewhere for orchids and probably nectar; the females are common at *Cassia* and *Canavalia* in November-December. The other *Eufriesia* normally visit the Park for nectar or in passing but will appear at chemical baits in the Park and would appear there for orchids if the appropriate species grew there. *Euglossa viridissima* breeds in the Park and both sexes find their food there, but the males go outside of the Park for orchid chemicals. All the other species of *Euglossa* taken at chemical baits in the Park do not normally visit the Park but are drawn there by the baits; their orchids, mates and food plants are elsewhere. The nest parasites, *Exaerete frontalis* and *E. smaragdina*, parasitize *Eulaema polychroma* and *Eufriesia mexicana* (the only large euglossines to nest in the Park) and visit plants in and outside of the Park for nectar and orchid-produced chemicals.

In short, then, it appears the species-packing of euglossines in SRNP or in any single habitat have it contains is a complex matter. If we define the habitat of a species as where its nest is, then there are a little euglossine, two big euglossines and two parasitic euglossines in SRNP. However, a sample of SRNP males taken with chemical baits will normally include many transient species. Viewed the other way round, if one is to preserve the euglossine fauna that can be found in SRNP, then one will have to preserve a much larger area than the Park, and an area that contains other habitat types not found in the Park. At the opposite environmental extreme from SRNP, at a place clothed in evergreen rainforest such as Corcovado National Park in southwestern Costa Rica, the same problem may occur but on a smaller scale.

Some species of orchid-bees visit *Anthurium* (Araaceae) and/or rotting wood (or slime fluxes) where fungi are producing chemicals similar to those obtained from the orchids. Since *Anthurium* occurs nowhere near the Park, it cannot be a cause to visit the Park nor be an orchid substitute for those males taken at chemicals in the Park. Visitation of fungi that are producing chemicals that are useful to the bees is a possible cause for the presence of euglossines in SRNP but simply not likely. Such visitations are only rarely seen anywhere in tropical forest and I have never encountered one in SRNP.

There is a further complication that needs to be added to this hypothetical conceptualization of euglossine population structure. It is assumed that each orchid-bee species has an orchid somewhere that it pollinates but I do not feel that this is a reasonable expectation. According to the hypothesis I have proposed, the consistent appearance of certain species of bees at chemicals without pollinaria and in a habitat free of relevant orchids means that they have been attracted to a habitat where their orchid does not naturally occur while they were foraging for mates, nectar, or orchids, or just flying by. However, there is an alternative hypothesis. Such bees may simply be parasites of the system, visiting

euglossine-pollinated orchids but not being the right size, shape or behavior to pick up pollinaria. How many such parasites can be packed into a orchid-bee-orchid complex remains to be seen, but it could be substantial since the interaction is a mutualism.

Given that orchid-bees behave in SRNP as postulated, and that orchids with flowers are at low density, what structure can one postulate for a dioecious orchid-bee-orchid interaction that maximizes the fitness of each partner? The idealized orchid should produce flowers with chemicals of sufficient quality (value to the bee, perceptability and life span) to sweep in all the males over a large area, and run each bee through a flower on the inflorescence once, or at the most, twice. If no pollination occurs, the plant should then wait a period equal to that required for the orchid population in total to produce an equilibrium density of pollinaria on bees (both through putting pollinaria on bees and through mixing of these bees with the population at large). The orchid should then produce another inflorescence and repeat the process. The chemical should have the trait that the bee does not return to the inflorescence during the lifetime of the inflorescence. The arrival of repeat bees will lower the arrival rate of absolute arrival number of newcomers, bees that may have had weeks to pick up a pollinarium. The bee should get a maximum load with one visit, thereby minimizing the time it spends away from courtship. However, it must eventually use up the chemicals and need a second visit days or weeks later.

Acknowledgements— M. Bonoff, F. Chaves, A. Herre, and J. Peterson aided in making observations on the orchid bees, N. H. Williams, R. Dressler, D. Gladstone, G. Stevens, C. D. Michener, J. D. Ackerman, L. Kimsey and W. Hallwachs offered constructive criticism of the manuscript. The study could not have occurred without the facilities provided by Santa Rosa National Park. This study was supported by NSF DEB 77-04889 and the orchid was located by members of an EEI team.

References

- Crüger, H. 1865. A few notes on the fecundation of orchids and their morphology. — J. Linn. Soc. Lond. Bot. 8: 127–135.
- Darwin, C. 1877. The various contrivances by which orchids are fertilized by insects. — Second edition, revised. J. Murray, London.
- Dodson, C. H. 1962. Pollination and variation in the subtribe Catasetinae (Orchidaceae). — Ann. Missouri Bot. Gard. 49: 35–56.
- , Dressler, R. L., Hills, H. G., Adams, R. M., and Williams, N. H. 1969. Biologically active compounds in orchid fragrances. — Science 164: 1243–1249.
- Dressler, R. L. 1979. *Eulaema bombiformis*, *E. meriana*, and Müllerian mimicry in related species (Hymenoptera: Apidae). — Biotropica 11: 144–151.
- Evoy, W. H. and B. P. Jones 1971. Motor patterns of male euglossine bees evoked by floral fragrances. — Anim. Behav. 19: 579–584.

- Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. – *Science* 171: 203–205.
- and Liesner, R. 1980. Annotated check-list of plants of lowland Guanacaste Province, exclusive of grasses and lower plants. – *Brenesia* (in press).
- , DeVries, P. J., Higgins, M. L. and Kimsey, L. S. 1980. Seasonal and site variation in male euglossine bees arriving at chemical baits in a Costa Rican deciduous forest and rain forest. – *Ecology* (submitted).
- Michener, C. D., Winston, M. L. and Jander, R. 1978. Pollen manipulation and related activities and structures in bees of the family Apidae. – *Univ. Kans. Sci. Bull.* 51: 575–601.
- Pijl, L. van der and Dodson, C. H. 1966. *Orchid flowers: their pollination and evolution.* – Univ. Miami Press, Coral Gables, Florida.
- Williams, N. H. 1978. A preliminary bibliography on euglossine bees and their relationships with orchids and other plants. – *Selbyana* 2: 345–355.