The reproductive biology of five of the seven species of *Bellucia* (Melastomataceae) was investigated in Amazonia. Successful fruit set by *Bellucia* required floral visitation by bees. The flowers are produced continuously all year, and are visited by a wide variety of female bees, the principal pollinators being *Nycteis*, *Centris*, *Pellitopus*, *Epicharis*, *Euglossa*, *Dexone*, and *Osmia*. The floral attractants are color and the odor produced by the pollen, stamens, and petals; the source is pollen. Three species of *Bellucia* are self-incompatible and discriminate visitation behavior and each of phenological, morphological, or genetic barriers tend to hybridization between sympatric species of *Bellucia*, and no more than two species occur in the same habitat at any one locality. *Bellucia* produces berries with numerous small seeds, and is dispersed by birds, bats, monkeys, bats, squirrels, and ants. Seedling establishment requires full sunlight, and occurs on a variety of soil types. The reproductive strategy is integrated as that of a pioneer species.

**Introduction**

As part of an effort to understand evolutionary relationships in a small group of closely related species, the reproductive biology of *Bellucia* (Melastomataceae) was investigated. This neotropical genus comprises seven species, four of which are medium-sized trees, and the other three shrubs. The species differ from each other in inflorescence position, subgenus, and morphology of the calyx. All but two are common, wide-ranging species. The object of this study was to establish whether these species have diversified in critical aspects of phenology, pollination biology, breeding system, and some dispersal strategy.

**Distribution**

The distribution of the seven species is shown in Figure 1. *Bellucia* granulosaoides
occurs from southern Mexico to Bolivia and Mato Grosso, Brazil; *B. pentamera* covers a similar latitudinal span but has a more western distribution and does not reach the Guianas. *Bulliaea sequiloba* occurs at the south-western periphery of the Amazon basin, in Brazil and northern Bolivia; *B. dichotoma* is found in the central and eastern Amazon basin, and one shrub species, *B. acutata*, is confined to the savannah of Brazilian Amazonia, mainly along the Madeira river. A further two shrub species occur in Mato Grosso and adjacent Bolivia, and Terr. Fed. Amazonas in Venezuela, respectively (Rinner, in press). *Bulliaea* occurs on several islands in the Caribbean where it has been introduced; it has also been introduced in Africa and Asia (Stone, 1972; van Steenis, 1955).

Three species occur at elevations from sea-level to between 800 and 1600 meters; the other four are lowland species.

The four arborescent species grow in undisturbed and disturbed vegetation, and are tolerant of a range from sandy, well drained to waterlogged (1st least for part of the year) soils. The shrubs grow in savannahs which are subjected to regular burning and flooding. Logging, road-building, and pasturing have provided excellent habitats for the light-demanding species of *Bulliaea*. *B. dichotoma* and *P. grossularioides* are amongst the most important pioneer species in terms of numbers of individuals per area in central Amazonia. In extra Amazonian regions, *B. pentamera* is often found invading newly deforested land.

The species' ranges often overlap but no more than two species occupy the same

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*Fig. 1. Distribution of *Bulliaea*. Two additional species occur in Mato Grosso and adjacent Bolivia and in Terr. Fed. Amazonas in Venezuela, respectively.*

B. acutata

B. sequiloba

B. dichotoma

B. grossularioides

B. pentamera
Habitat at any one locality.

Phenology

The flowering periods of B. dichotoma, B. grossularioides, and B. acutata in the vicinity of Manaus were determined by periodic observations from October 1980 to November 1982 and April 1982 to November 1984. In addition, collaborators of the "Regional critical size of ecosystems" (NEF-WHF project Lovejoy et al., 1984) collected phenological data for B. dichotoma and B. grossularioides in the same area from 1981 to 1984. These three species flowered for lengthy periods or continuously throughout the year. During the beginning of the rainy season from about October to January there was a high abundance of new flower buds but little flowering occurred in all months of the year. Some individual trees of B. dichotoma flowered continuously for at least five years, others paused for several months at irregular intervals. Flowering within the species was thus partly asynchronous. In other parts of the range of B. grossularioides, this species either prefers the rainy season (Croat, 1978; Cavalcante, 1970) or shows no clearcut flowering period (Kossman, pers. comm.). According to local residents B. pentamera and B. angolensis flower all year round near Rio Branco and Cruzeiro do Sul (Acre, Brazil). The fruitless phenology is the same as the flowering phenology.

Near Manaus an average tree or shrub of Bellucia dichotoma, B. grossularioides, or B. acutata puts out ten to twenty-five fresh flowers per day.

Floral Morphology and Floral Cycle

All six species have very similar flowers (comp. Fig. 2 A, B). The flowers have five to eight pure white (in Bellucia dichotoma) or externally pink-flushed petals which vary slightly in length between the species. The tree species have flowers six to eight centimeters across, while the shrub species' flowers are three to four centimeters in diameter. The buds begin to split open in the evening and by sunrise the petals spread horizontally. Upon opening of the flowers, the ten to sixteen stamens form a compact ring around the style which then bends to the lower part of the flower (i.e., closer to the ground side of the flower) and comes to lie between the two stigmas with the style protruding from the ring of stamens (Fig. 2 A, B). The stigma is large (about 3-5 mm diam.) and sticky. The stamens are thick and have the anthers turned inward with the two minute anther ectex (thick) pointed slightly inward, too. The stamens are white except for a yellow margin externally at the base of the connective. In all species, the petals change color from white to brown on the second day of anthesis. The flowers do not close during the night and the flower parts are shed on the third day.

Fragrance is produced by the petals, the upper part of the filaments, the connective tissue, the upper section of the style, and the stigma (determined by neutral red staining; Vogel, 1963). The pollen has a more or less pale yellow color depending on the species and possesses the same fragrance. The perfume of Bellucia has been compared to that of Convulvaria majalis L. (lily of the valley; Convallariaeae), citronella (Cymbopogon nardus L.) (Bande; Poaceae), or pomegranate (Eugenia sp., Myrtaceae). No odor is perceptible to humans in Bellucia acutata, but visitor behavior described below suggests that Reproductive biology of...
some scent is produced by this species also. It is noteworthy that odor intensity is strongest in second day flowers which have changed color from white to brown. No nectar is produced by Bellucia flowers.

Fig. 2. A - Bellucia grossularioides, petals 22 mm long; B - Bellucia dichotoma to the left, petals 20 mm long, held next to a putative hybrid between B. grossularioides and B. dichotoma.
Aroiding Systems
Controlled pollination experiments were carried out with Bellucia grossularioides, B. dichotoma, and B. acuta near Manaus, Brazil. Results are given in Table 1.

<table>
<thead>
<tr>
<th>Bellucia species</th>
<th>no. of self-pollinated flowers</th>
<th>cross-pollinated flowers</th>
<th>Control flowers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>treated</td>
<td>fruit set</td>
<td>treated</td>
</tr>
<tr>
<td>dichotoma</td>
<td>4</td>
<td>70 00</td>
<td>76 17</td>
</tr>
<tr>
<td>grossularioides</td>
<td>3</td>
<td>12 00</td>
<td>75 15</td>
</tr>
<tr>
<td>acuta</td>
<td>3</td>
<td>15 00</td>
<td>25 12</td>
</tr>
</tbody>
</table>

Table 1. Results from pollination experiments on Bellucia near Manaus (1980-82 and 1984).

The strong self-incompatibility shown agrees with the general findings of Iwao et al. (1985) of self-incompatibility in a majority of the ornithophytic trees examined in neotropical forests. The tested species were incapable of anemopetony. The set type of stigmatic surface and the binucleate pollen (John Raven, 1983) suggest a geophytic determination of self-incompatibility (Netzhammer, 1977). Artificial pollination between B. grossularioides and B. dichotoma yielded fruit with few but viable seeds. Putative hybrid trees with intermediate morphological characters were found along roadsides in the vicinity of Manaus. They were vigorous but seemed to have few seed set. Their pollen was viable as judged by a few back-crossing experiments with one parent, which yielded fruits with seeds. Because of the long time period between fertilization, fruits maturity, and seed germination, viability of the seeds was not tested in this last experiment. The hybrids have flowers intermediate between the parents in number of floral parts (Fig. 2 B).

Pollination Mechanism and Pollination
Bellucia grossularioides, B. dichotoma, and B. acuta were observed for about 80 hours each at different times of the year from October 1980 to November 1983 and from April to November 1984. For Bellucia acuta observations were made near Manaus and in the natural savannas of Humaitá (upper Madeira River, Amazonas). Bellucia grossularioides was studied near Manaus and in the upper Rio Negro region of Brazil and Venezuela (in March 1980). Bellucia dichotoma was observed at Manaus and near Santarém in lower Amazon River, Pará. Limited observations were made on Bellucia pentamera near humaitá and Rio Branco (Acre) and on Bellucia amplaflora near Rio Branco.

Bellucia flowers were visited exclusively by female bees which collected pollen as food for their larvae. 27 species belonging to 11 genera were collected from flowers of the five Bellucia species (Table 3), where two Bellucia species occurred at the same locality they were visited by the same species of bees.

Nocturnal observations of Bellucia grossularioides and B. dichotoma showed that wasps (Ampica pallida) were the only visitors. They gleaned pollen grains from petals Reproductive biology of...
**Table 2. Bees collected on flowers of Bellisia acutata, B. acutiloba, B. dichotoma, B. grossularioides, and B. pentamera. For localities see explanation in text.**

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>SPECIES</th>
<th>LOCALITY</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>EXAEIDAE</strong></td>
<td>Omma flavescens (Klug)</td>
<td></td>
</tr>
<tr>
<td><strong>ANTHOPHRIDAE</strong></td>
<td>Centris illacina (Cockerell)</td>
<td>Xylocopa frontalis (Olivier)</td>
</tr>
<tr>
<td></td>
<td>Centris sp. nov.</td>
<td>Xylocopa tegulata Friese</td>
</tr>
<tr>
<td></td>
<td>Ptilotopus superbus (Ducks)</td>
<td>Xylocopa similis F. Smith</td>
</tr>
<tr>
<td></td>
<td>Epicharis conica F. Smith</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Epicharis rustica (Olivier)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Epicharis affinis F. Smith</td>
<td></td>
</tr>
<tr>
<td><strong>HALICTIDAE</strong></td>
<td>Augochloropsis tuberculata (F. Smith)</td>
<td></td>
</tr>
<tr>
<td><strong>APIIDAE</strong></td>
<td>Euulaena cf. mariana (Olivier)</td>
<td>Melipona fulva Lep. et thier</td>
</tr>
<tr>
<td></td>
<td>Euulaena nigrita Lep. et thier</td>
<td>Melipona compressipes</td>
</tr>
<tr>
<td></td>
<td>Euulaena moccaryi (Frieze)</td>
<td>manumensis Schwarz</td>
</tr>
<tr>
<td></td>
<td>Euglossa interrecta Latreille</td>
<td>Melipona rufiventris</td>
</tr>
<tr>
<td></td>
<td>Euglossa cf. ignita Smith</td>
<td>Lepeletier</td>
</tr>
<tr>
<td></td>
<td>Bombus spp.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Trigona daltatorreana Friese</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Trigona recurva F. Smith</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Trigona fulviventris fulviventris Guerin-Meneville</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Trigona hyalina brasieri Cockerell</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Trigona (Plebeia) sp.</td>
<td></td>
</tr>
</tbody>
</table>

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All bees aligned directly on the stamens and curved their bodies over a few or all of the stamens depending on size. All bees except for those of the genus Trigona employed a specific foraging technique to release pollen from the peridial anthers. They produced vibrations of their thorax with the indirect flight muscles (wings held closed over the back) which were transmitted via the insects' legs onto the anthers and caused a cloud of pollen to shoot out of the anther pores. For this to be effective, a firm grip and close contact between the bee's body and the anthers was essential. Bees used their mandibles, in addition to the legs, to hold onto the exterior upper part of the stamens, often Injury tissue in the process. Flowers that had been visited repeatedly showed brown necrotic stains on the connectives that would gradually fade until all around the antheroecium, these stains are caused by the smaller bees' turning between each basking period during a single visit.

Bellulca pollen grains are small (ca 15 μm), smooth, and dry. They adhere to the bee's abdomen and to a minor extent to the rest of their bodies. Thus there is no specificity of pollen placement. Due to their morphology, the bees cannot completely clean themselves, and persistent pollen residues are usually found in a longitudinal line in the sector of the abdomen, which is the region where the bee's body, when curved tightly over the antheroecium, contacts the large, sticky stigmas. At the same time, the stigma is completely covered by the bee's abdomen and thus is protected from the flower's own pollen. Pollen leaves the anthers only when they are vibrated at high frequencies, e.g., 400 Hz, which was the frequency of a tuning fork used to quickly dislodge large amounts of pollen by simply striking it and holding it to the anthers. Abee does not cause pollen to leave the anthers. Morphological separation of pollen and stigma (backpogony) completely precludes automatic falling in Bellulca flowers; bee visitations of the flowers are obligatory for fertilization of the ovules.

Both large and small bees vibrated the stamens in the described manner; however, only bees large enough to contact a particular Bellulca species' stigma were legitimate pollinators of that species. The very wide range in size of the bees visiting any one Bellulca species is illustrated by Figure 3 A.

Trapping behavior was exhibited by Xylocopa, Centris, Philoapis, Epeolus, and Halicta bees. An easily spotted large (3 cm long) individual with a bright red thorax (Centris sp. nov., the third bee from the left in the topmost row in Fig. 30) arrived at the tree under observation at 8:25, 8:30, 8:32, and 8:37 A.M., on consecutive days.

Analyses of the proportional composition of pollen loads of 13 bees of the five trapping genera mentioned above indicated high fidelity to Bellulca in individual foraging flights. These visitors carried almost pure loads of Bellulca pollen with a few grains of Xylocopa, Apis, and Lasioglossum which were probably visited for nectar. Additionally, Cassia (Fibonacci) pollen, for which the bees foraged in the same manner as for Bellulca pollen, i.e., without the peridial anthers, was present in two cases.

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Fig. 3. A - bees captured on Bellucia grossulariiferae near Manaus (Brazil); B. Bellucia grossulariifera fruits placed on a leaf; average fruit is 7.5 cm long.

On the average, a Bellucia dichotoma tree with seventy to twenty-three open flowers was visited by eight legitimate pollinators per hour during the period (8-10 A.M.) of most intensive bee activity (n = 8 hrs on four consecutive days in December 1980). These pollinators normally visited all fresh flowers on a tree before flying on to another.

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Individuals of *Bellucia* (as indicated by the pollen load composition). Along roadsides and in savannas, individual large bees could be found with binoculars. Visits to two co-occurring species on the same foraging trip were observed for the pairs *Bellucia* grossularioides - B. dichotoma and *B. pentamera* - B. grossularioides near Mauan s and near Ma wa respectively.

*Trigona* bees were frequently encountered on *Bellucia* flowers in all localities, but did not vibrate the stamens in order to obtain the pollen. Instead, they were pollen scavengers and robbers (depending on the species), showing a complex behavior described in detail previously (Hammer, 1983). *Trigona* bees were sometimes present in great numbers, working on a single flower for several minutes. The large bees did not alight on flowers that had individuals of *Trigona* on them, and thus these pollen scavengers may enhance inter-plant movement of legitimate pollinators.

Flowers of the previous day, distinguishable by their brown color, were not visited except by an occasional *Melipona* or *Trigona* bee. It is interesting to recall that second day flowers had a stronger scent than fresh flowers. Bees probably used scent in addition to visual clues to find the flowers. This became obvious when flowers of *Bellucia acutata*, that had been bagged in the bud stage with insect-proof white gauze the evening before anthesis, were approached by bees during the morning; they opened even though the flowers were not visible.

**Fruit Dispersal**

*Bellucia* fruits are pale green to yellow semi-globose berries about 2-3 x 2-5 x 3-5 cm in size (Fig. 3 B). Their slightly succulent pulp contains about 3000 small (0.5-1 mm long) brown seeds. Many of the fertilized and underfertilized flowers persist unchanged for eight to 25 days before development or abscission occurs. Fruit ripening is complete in about eight weeks and the seeds take five to twenty-five weeks to germinate. Because of the almost continuous flowering of *Bellucia* plants, fruits are available over most of the year in any particular area of the genus' range.

The berries have a faint, fruity odor and a slightly astringent taste. They are taken by a wide range of animals: monkeys (M. rosmarin, pers. comm.), birds (psitt., obs.), and bats (M. macula, pers. comm.), and — once they have fallen to the ground — by tapirs (labea, deca.), turtles (M. rosmarin, B. moskowitz, pers. comm.) and ants (pers. obs.). The fruits have been fed to monkeys and hogs and are sometimes eaten by humans.

Birds are not the principal consumers and seed dispersers of *Bellucia*; the fruits’ position, size, color, scent, and taste indicate that they are most effective at attracting mammals. The relative importance of the different dispersal classes will be an object of future studies.

In repeated experiments, germination rates of the seeds were low (ca. 10%). *Bellucia* saplings are light-demanding and attain reproductive maturity in four years.
Although extended flowering is not uncommon among tropical plants, continuous flowering, such as here documented for *B. dichotoma*, is rare (Janzen, 1967; Halté et al., 1995). Other species of *Bellucia* also flower for extended periods, and clear-cut flowering periods are absent in all of them. *Bellucia* individuals, having reached the reproductive stage, invest a large part of their energy into almost continuous production of flowers and fruits. Self-incompatibility, shown for the three species whose breeding system was tested, is generally regarded as disadvantageous for colonizing species such as the members of *Bellucia*: this may be balanced by the very high number of seeds per fruit, which makes simultaneous germination of several seedlings at a new site likely. Provided flowers are visited repeatedly, the sticky, large stigmatic surface may enhance reception of the amount of pollen needed to fertilize the numerous ovules and increase chances for pollen from different parents to be received. Obligate outcrossing in self-incompatible tropical tree species often is correlated with a high proportion of big, trailing bees among their flower visitors (Frankie et al., 1983).

The pollination syndrome found in *Bellucia* and all lowland melastomes observed so far (Renner, 1994 a, b) has been described in recent years from a number of other plant species with poricidal anthers (see Bruchmann, 1983, for a review). The majority of these plants have stamens which release pollen only when vibrated by bees. Applied to *Bellucia*, flowers, vibrating stamens is an efficient method for the bees to quickly gather large amounts of pollen, particularly because bees are able to start pollen harvesting immediately upon landing. *Bellucia* is different from many bee-pollinated flowers of other plant families, in that the stamens not only provide visual and olfactory clues but at the same time a landing platform; thus no orientation or further walking are necessary once the bee has landed. Pollen release and stigma receptivity are simultaneous in these flowers.

There is no indication of partitioning of pollinator resources by the sympatric *Bellucia* species. One may speculate that the conservation in floral morphology in *Bellucia* is the result of stabilizing selection, with their shared pollinators being the selective agent. The lack of divergence in floral morphology and the lack of temporal separations of the sympatric species' flowering periods, together with the observed indiscernible visitor behavior and lack of genetic interspecific barriers (at least in some sympatric species), result in constant hybridization. However, as noted again recently (Carson, 1985), the genetic coherence of a (plant) species' gene pool will not be seriously threatened by interspecific hybridization.

Species of *Bellucia* are characterized by superior reproductive ability and means of dispersal. They are specialized for occupation of transient habitats in physiological features such as their seedling's light requirements and ability to establish on a variety of soil types, and in vegetative traits such as the fast growth of the light wood. It appears that species occupying early phases in succession have a high reproductive effort, in this case in the form of a very large number of seeds, and a correspondingly high intrinsic rate of natural increase: reselected species in the sense of MacArthur and 206

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Wilson (1927). Most species of bellicula can be regarded as tropical weeds; their population grows predominantly in situations disturbed by man and with man's help Bellicula has spread to the Caribbean and the Old World tropics.

ACKNOWLEDGMENTS

My thanks are due to the following apologists: W. E. Zimmer (Tringa), R. C. Hackett (Ptychopolis), Edward Halstead (V. B. Braas), C. B. B. (Exegetes), I. Mauro (Heliconius), D. S. Bumps (Meliponini), R. Smiling (Costerian). Further I would like to thank N. G. A. Abey for use of laboratory facilities at the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus (Brazil) and the curators and staff at INPA for their helpfulness and kindness during my stay there.

RESULTS

Fourteen investigations, namely: the biology reproducing, some of the species of Bellicula (Heliconia), a single bat and several butterflies, are presented in this analysis. Para las plantas de Bellicula producidas frutos, são necessários conténor de duas espécies de Bellicula. As espécies são produzidas o ano todo e são visitadas por uma variedade de insetos e pássaros. Os principais visitantes são os abelhas dos gêneros Helixopa. Contra, Philindris, Epiblema, Euclaria e Dasy. As espécies atuam pelo ovo e pelo solo por meio de pólen, petas e estilos e pelos óvulos. As abelhas são acompanhadas por pássaros. Tais espécies de Bellicula são autóctonas Collection. Devido às várias localidades nas povos visitantes, a biodiversidade entre espécies é ampla. nunca foram encontradas mais de duas espécies no mesmo habitat na mesma localidade. O fruto de Bellicula é uma base com pequenas e numerosas plantas despertas por plantas, sementes, pecados, estes, jaborão e jardins. As plantas requerem sol pleno para se destacarem e crescerem sob várias tipos de solo. Consideramos a estratégia reprodução como geral de uma planta pioneira.

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