

ORCHID BEES DON'T NEED ORCHIDS: EVIDENCE FROM THE NATURALIZATION OF AN ORCHID BEE IN FLORIDA

ROBERT W. PEMBERTON¹ AND GREGORY S. WHEELER

Invasive Plant Research Laboratory, United States Department of Agriculture, Agricultural Research Service, 3225 College Avenue,
Fort Lauderdale, Florida 33314 USA

Abstract. Almost 200 species of orchid bees are the exclusive pollinators of nearly 700 specialized orchids in the neotropics. This well-known mutualism involves orchids, called perfume orchids, which produce species-specific blends of floral fragrances, and male orchid bees, which collect and use these fragrance compounds during their courtship. We report here the naturalization of an orchid bee, *Euglossa viridissima*, in southern Florida, USA, where perfume orchids are absent. Chemical analysis of the contents of the fragrance storage organs in the hind tibiae of 59 male bees collected in Florida identified 55 fragrance compounds, including 27 known from the perfumes of nine species of *E. viridissima*'s orchid mutualists in Mesoamerica. Aromatic leaves, such as basil, were found to be important surrogate sources of needed fragrance compounds in Florida. The bee's ability to live and become abundant in the absence of its orchid mutualists suggests that the orchid bee–perfume orchid mutualism may be facultative for the bees, even though it is obligatory for the orchids. This invasive bee visits and potentially pollinates the flowers of many plants in Florida, behavior that could promote the abundance of selected exotic and native species.

Key words: *Euglossa viridissima*; euglossine bees; fragrance compounds; invasive species; mutualism; naturalization; orchids; orchid bees; pollination.

INTRODUCTION

Orchid bees (Apidae: Euglossini), native from central Mexico to northern Argentina (Roubik and Hanson 2004), have attracted considerable attention because of the complex mutualism with the orchids that they pollinate and their beautiful iridescent coloration (Dodson et al. 1969, Dodson 1975, Dressler 1982, Cameron 2004). Perfume orchids employ specialized floral fragrances composed of unique blends of many compounds that attract particular bee species (often an array of species; Williams and Dodson 1972, Dressler 1982), and strangely shaped flowers that manipulate the bees to effect their pollination. These orchids offer no nectar, pollen, or other food rewards to the visiting bees, which are all males. Instead, the male bees are attracted to the volatile floral fragrances, which they collect from the surfaces of the flowers with the capillary brushes of their front tarsi. Collected chemicals are stored in spongy organs within the enlarged tibia on their hind legs and then apparently used as sexual perfumes during their courtship (Roubik and Hanson 2004, Eltz et al. 2005a) and possibly in territorial defense (Roubik and Hanson 2004). Although often elusive (Cameron 2004), euglossine bees are abundant and important pollinators of other plants in addition to orchids (Dressler 1982, Roubik and Hanson 2004), especially low-density plants

visited repeatedly by the widely foraging bees (Janzen 1971).

Although perfume orchids are completely dependent on euglossine bees, observations of male orchid bees collecting chemicals from non-orchid sources in their native areas has led some researchers to question how dependent the bees are on the orchids (Dressler 1982, Ackerman 1983, Whitten et al. 1993, Roubik and Ackerman 1987). The naturalization of an orchid bee in southern Florida, USA, where no perfume orchids occur, except as rare horticultural curiosities, provides a unique opportunity to understand the orchid bee–perfume orchid mutualism because these bees and orchids have not been previously separated in nature. We investigated how the bees can live without their orchid mutualists and what this independence suggests about the evolution of the mutualism.

METHODS

Bee identification and field ecology

Euglossa viridissima Friese (Hymenoptera: Apidae), which belongs to a large complex of mostly green euglossine bees, was identified using literature (Moure 1970, Dressler 1978, Roubik and Hanson 2004) and confirmed by R. Dressler. The abundance of *E. viridissima* in southern Florida, USA was determined with a eugenol chemical bait (Roubik and Hanson 2004), and timed observations of the bees' activity. A strip of blotter paper (~5 × 15 cm) was saturated with eugenol and suspended from a tree branch 1.5 m above the ground at a Fort Lauderdale, Florida, garden site,

Manuscript received 17 June 2005; revised 3 February 2006; accepted 3 February 2006. Corresponding Editor: M. D. Eubanks.

¹ E-mail: bobbpem@saa.ars.usda.gov

where the bees were regularly seen. Bees landing on the bait between 09:20 and 11:20 hours on 18 September 2004 were collected and counted. Timed observations of bee presence were made during two four-hour (08:00 to 12:00 hours) periods of a 4 × 5 m flower bed containing flowers (*Allamanda peruvianum*, *Ruellia brittoniana*, *Senna mexicana*, *Tecoma stans*, *Solanum wendlandii*, and *Stachytarpheta urticifolia*) frequently visited by the bee on 29 and 30 September 2004 at the same Fort Lauderdale garden site.

Observations to determine plant usage were made primarily on flowers and the leaves of aromatic plants in residential gardens, urban parks, and nature preserves in Broward County, particularly where the bee was found to be abundant. The area currently occupied by the bee in southern Florida was estimated from the geographic limits established during plant usage surveys. Some plants considered to be potentially important to euglossine bees (Dressler 1982, Roubik and Hanson 2004) were added to the Fort Lauderdale garden to increase the chances of seeing interactions with plants of actual or potential importance. *Clusia lanceolata*, an ornamental shrub native to tropical America, was added because female euglossine bees are known to visit *Clusia* flowers to collect the resin to construct their brood cells (Roubik and Hanson 2004). Two *Solanum* species were added because *Solanum*, along with *Senna* (*Cassia*) species, which were common in the areas of observation, are known to be pollen sources for female euglossine bees (Roubik and Hanson 2004). Observations (primarily buzz pollen gathering and visitation of flowers used by non-heliconine butterflies for nectar) were supplemented by euglossine bee resource-use information reported by Roubik and Hanson (2004) to interpret what food resources (nectar, pollen, or both) were collected from the flowers. In addition, flowering orchid plants, *Lycaste cochleata* and *Sobralia decora*, congeneric with orchids pollinated by euglossine bees, were exposed to the bee for single-day periods to observe potential visitation and/or pollination. Nativity of visited plants was determined primarily with Wunderlin and Hansen (2003) and Llamas (2003).

Collection and identification of fragrance compounds

Chemical analysis was used to identify the compounds within the tibiae of 59 male *E. viridissima* bees, including 53 collected from a eugenol bait, 3 gathering oils from basil (*Ocimum basilicum*), and 3 visiting *Stemmadenia littoralis* flowers, all in Broward County, Florida. They were analyzed individually, except for the bees collected from basil, which were pooled into a single sample. Single tibia from each bee were removed with a scalpel and subjected to ultrasonic extraction in *n*-hexane (50 µL) for 5 min. Foliar compounds from fresh leaves (100 mg) of aromatic plants were microwave (750 watts, 1 min) digested in ethanol (500 mL) and extracted in an equal volume of chloroform (Wheeler et al. 2003). Material extracted was identified by gas chromatograph/

mass spectrometer (GC/MS) using an Agilent 6890 instrument fitted with a HP (5% phenyl)-methylpolysiloxane (30 m × 0.25 mm, 0.25 micron film thickness; Agilent, Palo Alto, California, USA) fused silica open tubular column with helium at 36 cm/sec as a carrier gas, injector port (split 1:20) at 250°C, mass selective detector (Agilent 5973) at 250°C (source) and 150°C (quad) with transfer line 280°C and ion source filament voltage of 70 eV. Component identification was made on the basis of mass spectral fragmentation, retention index with *n*-paraffins, comparison with authentic constituents when available, and mass spectral and retention matching with commercial libraries (NIST, Wiley, and Adams). Identified compounds were compared to fragrance compounds reported to occur in the bees' orchid mutualists.

RESULTS

We first observed *E. viridissima* (Plate 1) collecting pollen from *Begonia odorata* flowers in Fort Lauderdale during the summer 2003, and the first specimen of the bee was collected 12 June 2003. In August 2004, we identified the bee and began intensive studies. This orchid bee, which is native to central Mexico south to western Costa Rica (Moure 1970), occurs within an area of at least 650 km² in Broward and Palm Beach Counties in southeastern Florida, USA. *Euglossa viridissima* may also be established in adjacent Miami-Dade County because two males were found in a USDA Jackson trap in the county on 28 May 2004 (Skov and Wiley 2005). The bee is irregularly distributed within Broward and Palm Beach Counties and is commonly encountered in residential gardens and city parks. It has also invaded natural areas and is frequently seen on native beach, coastal strand, and hardwood hammock communities. The bee can be abundant: even more so than reported for its native region, where it is one of the most abundant *Euglossa* species (Janzen et al. 1982). A single eugenol bait placed in a residential garden where the bee is regularly seen, attracted 52 male *E. viridissima* in two hours, or 26 bees/hour. The average capture rate at 18 site-date collections with eugenol baits in its native Costa Rica was 7.9 bees/hour (calculated from Janzen et al. 1982). Continuous timed observations also indicate that *E. viridissima* is abundant and is foraging intensively in Florida. The bee was recorded to visit flowers within a 5 × 6 m garden plot almost half the time during the monitoring periods (43.8% and 44.5% of the two 08:00 to 12:00 morning periods in September). Seven plant species were foraged, with female bees buzz collecting pollen from *Senna mexicana* accounting for half the foraging time. Nectar collection from the gullet type flowers (Dressler 1982), *Ruellia brittoniana* and *Tecoma stans*, accounted for most of the rest. *E. viridissima* was the most common flower visitor in the plots.

Our gas chromatograph/mass spectrometer (GC/MS) analyses of the contents of the tibia of the 59 male bees identified 55 compounds, including 27 known floral

fragrance components of nine orchid species visited by *E. viridissima* in its native Mexico and Costa Rica (Fig. 1). Perfume orchids visited by this bee were reported by Roubik and Hanson (2004), and their fragrance chemistry has been elucidated by Gregg (1983), Gerlach and Schill (1991), Whitten and Williams (1992), and Kaiser (1993). Our bee tibia collections included 17 compounds reported for *Lycaste aromatica* and 12 for *L. cruenta* (Kaiser 1993), comprising >85% of the total fragrance abundance in these species. For *L. aromatica*, the major floral compounds we found and their reported relative abundance (Kaiser 1993) were methyl (*E*)-cinnamate (45.5%), (*E*)- β -ocimene (36%), and eugenol (1.4%). For *L. cruenta* they were (*E*)- β -ocimene (44%), methyl (*Z*)-*p*-methoxycinnamate (18.5%), linalool (12.2%), and methyl (*E*)-*p*-methoxycinnamate (6.9%) (Kaiser 1993). Sixteen of the recovered compounds are known floral fragrance components of *Gongora armeniaca*, including (*E*)- β -ocimene (22%), germacrene D (17.5%), caryophyllene (13.1%), and hydroquinone dimethyl ether (6.1%) (Kaiser 1993). Recovered compounds were also major components of the floral fragrances of *Cynoches egertonianum* (Gregg 1983), *Notylia barkeri* (Gerlach and Schill 1991), and two *Stanhopea* species, *S. radiosa* and *S. saccata* (Whitten and Williams 1992). In contrast to our recovery of many compounds reported from the bees' mutualist orchids, which produce chemically diverse perfumes, we did not recover compounds reported from the mutualist orchids that produce only one or a few compounds; e.g., *S. tigrina* (Whitten and Williams 1992), *Houlletia tigrina*, and *Coeliopsis hycinthosma* (Gerlach and Schill 1991). Major orchid compounds, such as α -pinene, myrcene, 1,8-cineole, (*Z*)- β -ocimene, linalool, β -caryophyllene, germacrene D, methyl (*Z*)-*p*-methoxycinnamate, and methyl (*E*)-*p*-methoxycinnamate, were found in >20% of the bees. The bees had 9.6 ± 1.2 (mean \pm SE) perfume orchid compounds (range = 0–35). Three relatively minor compounds were found in only one bee, 15 occurred in >20% of the bees, and three occurred in >50% of the bees.

Aromatic leaves appear to be important sources of perfume orchid compounds for the bees in Florida. *Euglossa viridissima* males were observed gathering fragrant oils from basil (*Ocimum basilicum*; see Plate 1) and allspice (*Pimenta dioica*) leaves. The leaves of an introduced tree, melaleuca, *Melaleuca quinquenervia*, are apparently also visited because viridiflorol, a compound whose only known south Florida source is this melaleuca, was found in the bee tibia. Our analyses (Fig. 2) indicate that *M. quinquenervia* leaves have 17 of the 27 perfume compounds in the bee tibia, whereas basil and allspice have 5 and 7, respectively, including many major compounds such as *E*- β -ocimene and eugenol. Compounds reported from a more detailed analysis of basil leaves (Sacchetti et al. 2004) include 14 of the recovered 27 perfume compounds, including methyl (*Z*) cinnamate. Analysis of the tibial contents of



PLATE 1. *Euglossa viridissima*, a Mesoamerican orchid bee recently naturalized in Florida, USA. The photo shows a male bee gathering "orchid" perfume compounds from a sweet basil (*Ocimum basilicum*) leaf (note his enlarged hind tibia, which stores collected compounds). Photo credit: R. W. Pemberton.

four bees that collected oils from the sweet basil and globe basil varieties found nine perfume orchid compounds (see Fig. 2 for the chromatograms of compounds extracted from a representative bee tibia and the leaves of sweet basil, allspice, and melaleuca).

Collection of the fragrance oils involved the bee grasping a leaf, and then lightly chewing the margins and/or principal veins, while secreting lipid compounds from their labial glands (Cameron 2004, Whitten et al. 1989) to dissolve the oils, which were mopped up with their capillary tarsal brushes. After 15–30 seconds of extracting compounds from a leaf, the bee would hover and transfer the chemicals to its tibial organs, before landing again to repeat the process, typically for another 15 minutes. During the six times that the bees were observed gathering oils from basil, three occurrences involved several bees making nearly simultaneous collections.

We observed *E. viridissima* visiting the flowers of 45 species of plants in 18 families in Florida, including 42 to obtain nectar and/or pollen (Table 1). Many of the visited plants (*Allamanda*, *Ipomoea*, *Ruellia*, *Stemmadenia*, *Tabebuia*, and *Tecoma* species) have gullet flowers into which the bees crawl to feed, primarily on nectar. Nineteen plants (*Begonia*, *Commelina*, *Dichorisandra*, *Tradescantia*, *Senna* [*Cassia*]), and *Solanum* species) were visited by females exclusively for pollen; *Senna* and *Solanum* species were buzzed to collect pollen. We observed female bees collecting resin from the flowers of *Clusia lanceolata*, an exotic ornamental shrub, every day during good weather for several months. The flowers of *Clusia* species are well-known sources of resin for female euglossine bees (Roubik and Hanson 2004). Two of the exposed test orchids, one *Lycaste cochleata* plant exposed for one day and two *Sobralia decora* plants

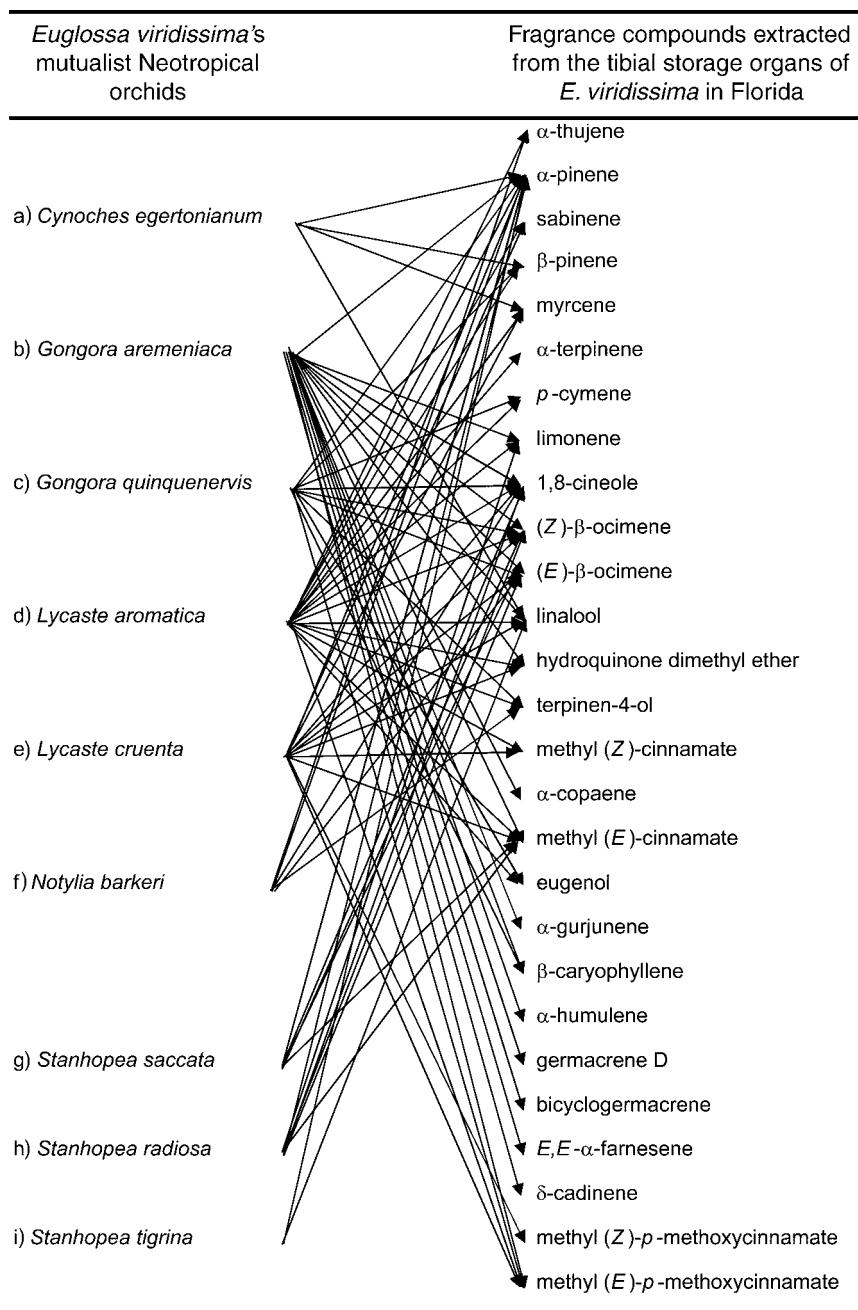


FIG. 1. Perfume compounds collected by male *Euglossa viridissima* in Florida, USA, and their occurrence in the bees' orchid mutualists in Mexico and Central America. Absent are mutualist orchids visited by the bees, because either their exact identity or their fragrance chemistry is unknown, including species of *Catasetum*, *Chondrorhyncha*, *Dressleria*, *Gongora*, *Lycaste*, *Mormodes*, and *Trichocentrum* (Roubik and Hanson 2004). Many *Catasetum* and *Mormodes* species also have the compounds collected by the bee in Florida (Gerlach and Schill 1991).

exposed for one day each, were visited. A single bee of unknown gender briefly visited the *L. cochleata*, but the pollinia were not removed. Female bees visited both *S. decora* plants, and during one visit, a bee removed a pollinarium, carried it on her thorax for about an hour, and then revisited the plant and pollinated a flower. *Lycaste* species are visited by *E. viridissima* in its native

area, and *Sobralia* species are known to be visited by euglossine bees (Roubik and Hanson 2004). Many *Lycaste* species are perfume orchids, but *Sobralia* species are apparently not, because they offer nectar rewards (van der Pijl and Dodson 1969). The absence of food rewards in perfume orchids probably limits visitors to male euglossine mutualists.

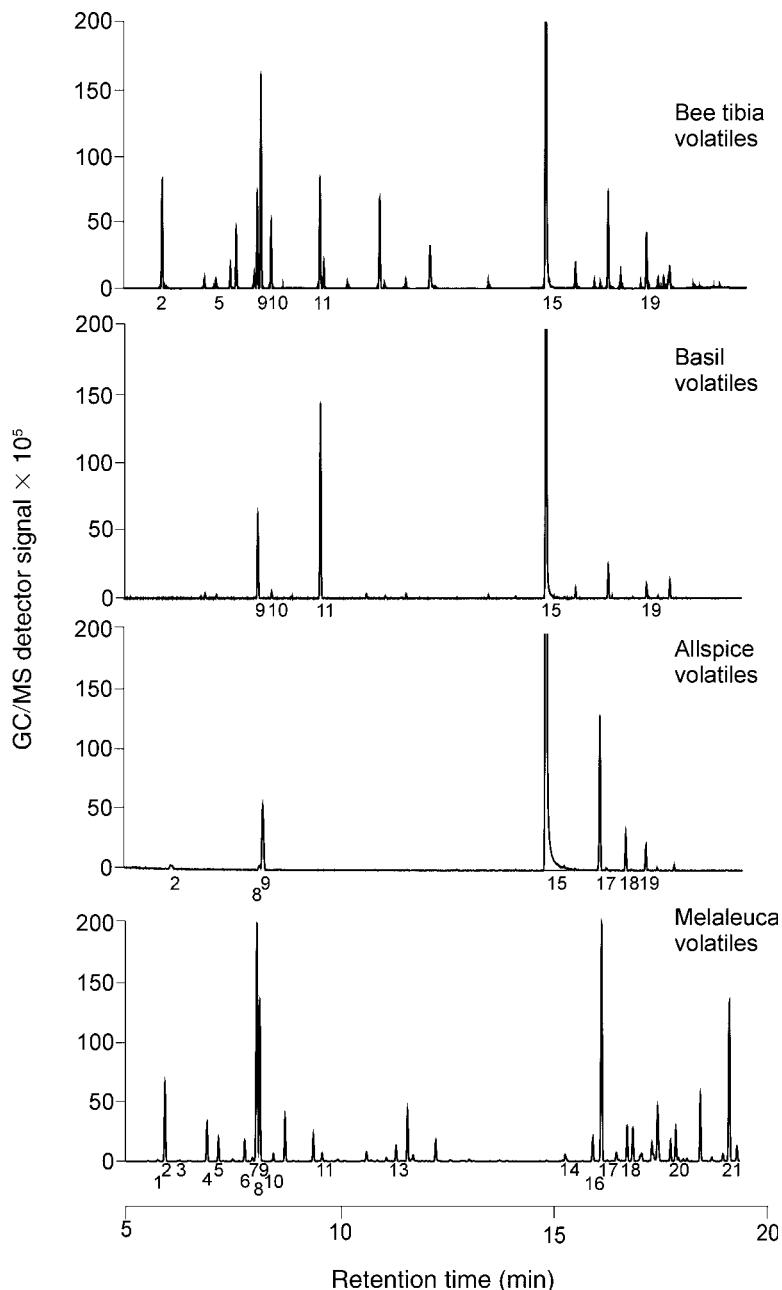


FIG. 2. Gas chromatographic/mass spectrometer (GC/MS) analysis of the contents of a hind tibial storage organ from a representative *E. viridissima* bee that had visited globe basil (*Ocimum basilicum*), and potential plant sources of perfume compounds recovered from bee tibia including: 1, α -thujene; 2, α -pinene; 3, sabinene; 4, β -pinene; 5, myrcene; 6, α -terpinene; 7, *p*-cymene; 8, limonene; 9, 1,8-cineole; 10, (*Z*)- β -ocimene; 11, (*E*)- β -ocimene; 12, linalool; 13, terpinen-4-ol; 14, α -copaene; 15, eugenol; 16, α -gurjunene; 17, β -caryophyllene; 18, α -humulene; 19, germacrene D; 20, δ -cadinene; and 21, viridiflorol.

DISCUSSION

E. viridissima is able to live in Florida because it obtains all four types of needed plant resources, including fragrance compounds for males, nectar for energy for both sexes, and pollen and resin for females to construct and provision their brood cells.

Prior to *E. viridissima*'s naturalization in Florida, there has been no opportunity to learn if euglossine bees

could live without their orchid mutualists. The observation of male euglossine bees collecting perfume compounds from fungus infected logs (Whitten et al. 1993), and from non-orchid flowers, as well as the infrequent occurrence of orchid pollinia on trapped bees (Ackerman 1983), led these authors and others (Dressler 1982, Roubik and Ackerman 1987, Roubik and Hanson 2004) to question the degree of dependency of these bees on

TABLE 1. Plants visited by *Euglossa viridissima* in Florida, USA, and the products collected (plants are arranged by families to illustrate family usage).

Family	Plant species	Plant type	Collected products
ACANTH	<i>Asystasia gangetica</i>	invasive-horticultural	nectar
ACANTH	<i>Ruellia brittoniana</i>	invasive-horticultural	nectar
APOCY	<i>Allamanda neriiifolia</i>	horticultural	nectar, pollen
APOCY	<i>Mandevilla</i> hybrid	horticultural	nectar, pollen
APOCY	<i>Stemmadenia litoralis</i>	horticultural	nectar, pollen
APOCY	<i>Thevetia</i> sp.	horticultural	nectar, pollen
BEGON	<i>Begonia coccinea</i>	horticultural	pollen
BEGON	<i>Begonia odorata</i>	horticultural	pollen
BIGNON	<i>Tabebuia aurea</i>	horticultural	nectar
BIGNON	<i>Tabebuia heterophylla</i>	invasive-horticultural	nectar
BIGNON	<i>Tecoma stans</i>	naturalized-horticultural	nectar, pollen
CLUS	<i>Clusia lanceolata</i>	horticultural	floral resin
COMMEL	<i>Commelina erecta</i>	native	pollen
COMMEL	<i>Dichorisandra thyrsiflora</i>	horticultural	pollen
COMMEL	<i>Tradescantia spathacea</i>	native	pollen
COMMEL	<i>Tradescantia pallida</i>	naturalized-horticultural	pollen
CONVOL	<i>Ipomoea indica</i>	native?	nectar, pollen
CONVOL	<i>Ipomoea pes-caprae</i>	native	nectar, pollen
CUCURB	<i>Momordica charantia</i>	naturalized weed	pollen
FAB	<i>Clitoria ternata</i>	horticultural	nectar
FAB	<i>Canavalia rosea</i>	native	nectar, pollen
FAB	<i>Senna alata</i>	naturalized-horticultural	pollen
FAB	<i>Senna ligustrina</i>	native	pollen
FAB	<i>Senna mexicana</i>	native	pollen
FAB	<i>Senna occidentalis</i>	naturalized weed	pollen
FAB	<i>Senna pendula</i>	invasive-horticultural	pollen
FAB	<i>Senna surattensis</i>	naturalized-horticultural	pollen
FAB	<i>Senna</i> sp.	horticultural	pollen
LAM	<i>Ocimum basilicum</i>	horticultural	leaf chemicals
LAM	<i>Salvia</i> sp.	horticultural	nectar, pollen
MELAST	<i>Dissotis rotundifolia</i>	horticultural	pollen
MELAST	<i>Tibouchina urvilleana</i>	horticultural	pollen
MYRT	<i>Pimenta dioica</i>	horticultural	leaf chemicals
ORCHID	<i>Lycaste cochleata</i>	horticultural	?
ORCHID	<i>Sobralia cultivar</i>	horticultural	nectar
RUB	<i>Hamelia longipes?</i>	horticultural	nectar, pollen
RUB	<i>Hamelia patens</i>	native-horticultural	nectar, pollen
RUB	<i>Ixora coccinea</i>	horticultural	nectar
SOLAN	<i>Cestrum diurnum</i>	invasive-horticultural	nectar?
SOLAN	<i>Solanum wendlandii</i>	horticultural	pollen
SOLAN	<i>Solanum viarum</i>	invasive-weed	pollen
VERB	<i>Lantana camara</i>	invasive-horticultural	nectar
VERB	<i>Stachytarpheta jamaicensis</i>	native	nectar, pollen
VERB	<i>Stachytarpheta urticifolia</i>	naturalized-horticultural	nectar, pollen
VERB	<i>Stachytarpheta</i> large purple	horticultural	nectar, pollen
ZING	<i>Monocostus uniflorus</i>	horticultural	nectar

Notes: Family codes: ACANTH, Acanthaceae; APOCY, Apocynaceae; BEGON, Begoniaceae; BIGNON, Bignoniaceae; CLUS, Clusiaceae; COMMEL, Commelinaceae; CONVOL, Convolvulaceae; CUCURB, Cucurbitaceae; FAB, Fabaceae; LAM, Lamiaceae; MELAST, Melastomaceae; MYRT, Myrtaceae; ORCHID, Orchidaceae; RUB, Rubiaceae; SOLAN, Solanaceae; VERB, Verbenaceae; and ZING, Zingiberaceae. Species and genera native to Florida and the American tropics are in boldface type. No chemical collection was observed in the temporarily exposed orchids.

their orchids. Although the orchids are completely dependent on the bees for pollination, these observations have raised doubt about coevolution between the bees and the orchids. Our findings demonstrate that an orchid bee can not only survive, but thrive, in the absence of its mutualistic orchids. The uniqueness of perfume orchid fragrances is not in producing unique compounds (Williams 1978), since biosynthetic pathways for production of these chemicals have evolved in many different plant groups (Roubik and Hanson 2004), but in the larger amounts and in particular blends that are powerful attractants to the euglossine bees (Gerlach and Schill 1991). These factors suggest that perfume

orchids evolved in response to the bees' foraging for particular volatile chemicals and that coevolution between these bees and their orchids did not occur or was more one-sided than generally assumed.

Our finding that, in Florida, *E. viridissima* collects a remarkably similar suite of compounds to those occurring in its orchid mutualists in the neotropics strongly suggests that euglossine bees are using species-specific compounds. A recent study (Eltz et al. 2005b), which found that males of three *Euglossa* species living in different parts of their geographic ranges collect the same suite of chemicals, also indicates the species-specific nature of the scent collection.

Although this study can tell us relatively little about the role of *E. viridissima* in Florida, it could have pervasive ecological effects, because this species is abundant and interacts with many other species. Observed flower visitation suggests that *E. viridissima* is a potential pollinator of selected native, ornamental, naturalized, and invasive plant species. Pollination of introduced plants that are pollinator limited could increase their abundance and invasiveness (Parker 1997). This scenario occurred recently with two ornamental figs, *Ficus altissima* and *F. microphylla*, in Florida. These figs were sterile, noninvasive ornamentals, which became aggressive invaders following the accidental introduction of their pollinating wasps (Nadel et al. 1992). The bee may interact with native and exotic pollinators whose presence and behaviors it could alter, as demonstrated by the naturalized honeybee (Roubik 1978). Potential environmental effects aside, the presence of the bee in Florida and its ability to live independently of perfume orchids changes our understanding of the orchid bee–perfume orchid mutualism.

ACKNOWLEDGMENTS

We thank J. Blackmere and R. Dressler for assistance related to determining the bees' identities; H. Liu for discussion on flower visitation; and J. Ackerman, R. Dressler, H. Liu, D. Roubik, M. Whitten, and N. Williams for helpful reviews of an earlier draft of the manuscript.

LITERATURE CITED

- Ackerman, J. D. 1983. Specificity and mutual dependence of the orchid-euglossine bee interaction. *Biological Journal of the Linnean Society* **20**:340–314.
- Cameron, S. A. 2004. Phylogeny and biology of neotropical orchid bees (Euglossini). *Annual Review of Entomology* **49**: 377–404.
- Dodson, C. H. 1975. Coevolution of orchids and bees. Pages 91–99 in L. E. Gilbert and P. H. Raven, editors. *Coevolution of animals and plants*. University of Texas Press, Austin, Texas, USA.
- Dodson, C. H., R. L. Dressler, H. C. Hills, R. M. Adams, and N. H. Williams. 1969. Biologically active compounds in orchid fragrances. *Science* **164**:1243–1249.
- Dressler, R. L. 1978. An infrageneric classification of *Euglossa*, with notes on some features of special taxonomic importance (Hymenoptera; Apidae). *Revista de Biologia Tropical* (San Jose, Costa Rica) **26**:187–198.
- Dressler, R. L. 1982. Biology of the orchid bees (Euglossini). *Annual Review of Ecology and Systematics* **13**:373–394.
- Eltz, T., D. W. Roubik, and K. Lunau. 2005a. Experience-dependent choices ensure species-specific fragrance accumulation in male orchid bees. *Behavioral Ecology and Sociobiology* **59**:149–156.
- Eltz, T., A. Sager, and K. Lunau. 2005b. Juggling with volatiles: exposure of perfumes by displaying male orchid bees. *Journal of Comparative Physiology A* **191**:575–581.
- Gerlach, G., and R. Schill. 1991. Composition of orchid scents attracting Euglossine bees. *Botanica Acta* **104**:379–391.
- Gregg, K. B. 1983. Variation in floral fragrances and morphology: incipient speciation in *Cynoches*. *Botanical Gazette* **144**:566–576.
- Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* **171**:203–205.
- Janzen, D. H., P. J. De Vries, M. L. Higgins, and L. S. Kimsey. 1982. Seasonal and site variation in Costa Rican euglossine bees at chemical baits in a deciduous forest and an evergreen forest. *Ecology* **63**:66–74.
- Kaiser, R. 1993. *The scent of orchids, olfactory and chemical investigations*. Elsevier, Amsterdam, The Netherlands.
- Llamas, K. L. 2003. *Tropical flowering plants*. Timber Press, Portland, Oregon, USA.
- Moure, J. S. 1970. The species of Euglossine bees of Central America belonging to the Subgenus *Euglossella* (Hymenoptera, Apidae). *Anais da Academia Brasileira de Ciências* (Rio de Janeiro) **42**:147–157.
- Nadel, H., H. Frank, and R. J. Knight. 1992. Escapees and accomplices: the naturalization of exotic *Ficus* and their associated faunas in Florida. *Florida Entomologist* **75**:29–39.
- Parker, I. M. 1997. Pollinator limitation of *Cytisus scoparius* (scotch broom), an invasive exotic shrub. *Ecology* **78**:1457–1470.
- Roubik, D. W. 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. *Science* **201**: 1030–1032.
- Roubik, D. W., and J. D. Ackerman. 1987. Long-term ecology of euglossine orchid-bees (Apidae: Euglossini). *Oecologia* **73**: 321–333.
- Roubik, D. W., and P. E. Hanson. 2004. *Orchid bees of tropical America, biology and field guide*. Instituto Nacional de Biodiversidad, San Jose, Costa Rica.
- Sacchetti, G., A. Medici, S. Maietti, M. Dadice, M. Muzzoli, S. Manfredini, E. Braccioli, and R. Bruni. 2004. Composition and functional properties of essential oil of Amazon basil, *Ocimum micranthum* Willd., Labiate, in comparison with essential oils. *Journal of Agricultural and Food Chemistry* **52**:3486–3491.
- Skov, C., and J. Wiley. 2005. Establishment of the Neotropical orchid bee *Euglossa viridissima* (Hymenoptera: Apidae) in Florida. *Florida Entomologist* **88**:225–227.
- van der Pijl, L., and C. H. Dodson. 1969. *Orchid flowers; their pollination and evolution*. University of Miami Press, Coral Gables, Florida.
- Wheeler, G. S., L. M. Massey, and I. A. Southwell. 2003. Dietary influences on terpenoids sequestered by the biological control agent *Oxyops vitiosa*: effect of plant volatiles from different *Melaleuca quinquenervia* chemotypes and laboratory host species. *Journal of Chemical Ecology* **29**: 188–207.
- Whitten, W. M., and N. H. Williams. 1992. Floral fragrances of *Stanhopea* (Orchidaceae). *Lindleyana* **7**:30–153.
- Whitten, W. M., A. M. Young, and D. L. Stern. 1993. Nonfloral sources of chemicals that attract male Euglossine bees (Apidae: Euglossini). *Journal of Chemical Ecology* **19**: 3017–3027.
- Whitten, W. M., A. M. Young, and N. H. Williams. 1989. Function of the glandular secretions in fragrance collection by male euglossine bees (Apidae: Euglossini). *Journal of Chemical Ecology* **15**:1285–1295.
- Williams, N. H. 1978. A preliminary bibliography on euglossine bees and their relationships with orchids and other plants. *Selbyana* **2**:345–355.
- Williams, N. H., and C. H. Dodson. 1972. Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long distance pollen flow. *Evolution* **26**:84–95.
- Wunderlin, R. P., and B. F. Hansen. 2003. *Guide to the vascular plants of Florida*. University Press Florida, Gainesville, Florida, USA.