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POLLINATION OF THE ORNAMENTAL ORCHID *ONCIDIUM SPHACELATUM* BY THE NATURALIZED OIL-COLLECTING BEE (*CENTRIS NITIDA*) IN FLORIDA

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ABSTRACT. The recently naturalized oil-collecting bee *Centris nitida* pollinates the cultivated *Oncidium sphacelatum* in southern Florida. Female *C. nitida* bees seeking food are the pollinators of this food deceit orchid, which appears to mimic species of Malpighiaceae, which have oil rewards collected by the bee. The fruit set rate ranged from 0.54% to 3.0% and averaged 1.49%, which is many times higher than the 0.0% and 0.25% reported for this orchid in its native Mexico. The many capsules produced (66 fruits in the three large exposed plants in this study) contain many millions of seed. The large number of seeds produced could promote the naturalization of *O. sphacelatum* in Florida if suitable mycorrhizae are present. *Centris nitida* and *O. sphacelatum* are broadly sympatric in tropical America and may interact in their native area. *Centris nitida* and *Euglossa viridissima* (an orchid bee which has also recently naturalized in southern Florida) are participants in pollination webs involving many plants including native, ornamental, naturalized, and invasive plants.

Key words: bee, deception orchid, naturalized, pollination, rewardless flowers

Oncidium sphacelatum Lindl. is a popular ornamental orchid that is frequently cultivated out-of-doors in southern Florida. Known as one of the dancing doll orchids, it is native to Mexico, to Costa Rica, and Venezuela (Pridgeon 1994). Its bright yellow flowers, barred with brown markings, are nectarless and have little fragrance to the human nose. Solitary oil-collecting bees in the genera *Centris* and *Tetrapedia,* and stingless bees *Trigona* (Apidae) are reported to be pollinators of *Oncidium* species (van der Cingel 2001, Alcantara et al. 2006). *Oncidium sphacelatum* was recently reported to be pollinated by *Centris* bees in Mexico (Damon & Cruz-Lopez 2006).

On March 8, 2007 at about 12:30 pm, I captured a *Centris nitida* Smith in a Ft. Lauderdale, Florida garden with an orchid pollinarium on its face. The captured bee was a female gathering the edible oil reward from the flowers of the native Florida shrub *Brysonima lucida* (Mill.) DC. (Malpighiaceae), which was planted in the residential garden. The bee with the pollinarium was captured as part of an effort to obtain specimens of *C. nitida,* which I had discovered to be a recently naturalized bee in southern Florida and native to the Neotropics (Pemberton & Liu 2008). The pollinarium appeared to be from an *Oncidium* species; three large baskets of flowering *O. sphacelatum* plants were in the same garden, about 15 meters from the shrub where the bee was captured. I made a specimen of the bee, and then removed pollinia from several flowers from the *O. sphacelatum* plants for comparison, and found the pollinia from the flowers to be identical in size and shape to the pollinarium borne by the bee (FIGURE 1). In addition, all three *O. sphacelatum* plants bore mature fruits from the previous year's flowering, suggesting that pollination was occurring in the plants.

The presence of the pollinarium on the face of *C. nitida* strongly suggested that the bee is a pollinator of the plant. A small study was undertaken to examine the interactions of *C. nitida* and *O. sphacelatum,* which broadly co-occur in tropical America. I manipulated flowers to learn about the breeding system of the plant in order to better interpret the bee-flower interaction. I also determined which of the several previously described *Centris-Oncidium* pollination syndromes (van der Cingel 2001) was involved with the *C. nitida-O. sphacelatum* interaction.

METHODS

Brief timed watches were made of two plants in an attempt to observe *C. nitida* visitation of *O. sphacelatum* flowers on the two large blooming plants in large baskets in the Ft. Lauderdale residential yard. Observations of exposed pollinia and pollinia falling onto or near the stigmas of some flowers suggested that self pollination may occur. Potential apomixis and self pollination were examined in these plants by bagging

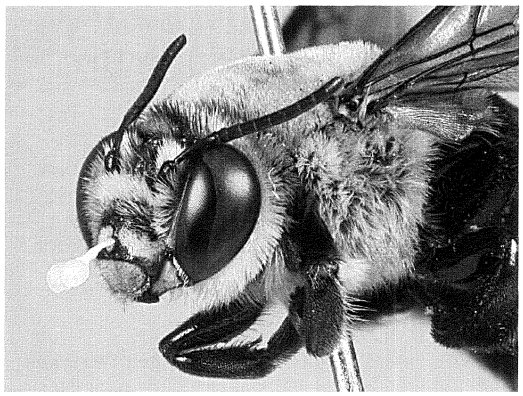

FIGURE 1. Female of the naturalized oil-collecting bee (*Centris nitida*) bearing a pollinarium of the ornamental orchid (*Oncidium sphacelatum*) on her face.

eight inflorescences and three additional inflorescence tips prior to flower opening and maintaining the bags until the flowering finished. I also tagged 10 flowers with intact anther caps and 10 flowers without anther caps to detect changes in anther caps and the exposed pollinia. Supplementing these treatments was the maintenance of a single plant with seven inflorescences in an insect proof screen house during its entire bloom.

Male reproductive function was assessed by counting the number of flowers without anther caps (missing anther caps implying pollinaria removal by pollinators) in two inflorescences, one from each plant on April 22, and seven inflorescences (two old, and five young) on second flowering pulse on one of the plants on June 2. Female reproductive success was assessed on May 26 and 31 at the end of the flowering period for two of the plants and near the end for the third plant, when all old inflorescences were cut from the plants. The persistent bracts that subtend individual flowers were counted to obtain the total number of flowers borne on each inflorescence, along with the number of fruit forming, so that the percent of pollination success could be calculated per inflorescence and plant.

RESULTS

Flowers on two large plants were watched at mid-day on March 12 (1:35–3:00 pm), April 1 (1:30–2:30 pm), and April 5 (12:34–1:21 pm and 2:24–2:34 pm) for a total of 205 minutes. On March 12 the only visitors to appear were two *Euglossa viridissima* which hovered briefly before flowers. During the April 1 watch, six *C. nitida* visited at least 23 flowers, mostly moving flower to flower briefly touching the lips, and landing on only a few. No pollinia removal was observed. Precise observation was difficult because of the bees' rapid movement and many large inflorescences with abundant flowers on two plants. A single honey bee also visited during the April 1 watch, but did not remove the pollinia. On April 5 at 12:54 pm, one female *C. nitida* was observed to visit five flowers on two plants and removed a pollinarium from a flower before being captured. The pollinarium was placed in the middle of her face in the same manner as the *O. sphacelatum* pollinarium on the other bee captured on *B. ludida* flowers on March 8.

Of 10 tagged flowers with intact anther caps, six lost their caps after two days and two self pollinia were found on or near the stigmas of the flowers that produced them. Two anther caps from these flowers were found on the stigmas. Of the 10 tagged flowers with missing anther caps but with erect pollinaria, four of the falling pollinia were missing and another leaning downward near the stigma two days later. None of these flowers set fruit. The assessment of flowering inflorescences for male success found 32 of 213 (15%) anther caps missing from flowers on the two inflorescences evaluated on April 22. The June 2 evaluation found that neither of the two older inflorescences (which had no buds and some aging flowers) had any anther caps remaining in the 37 flowers, while the five younger inflorescences, (which had some unopened flower buds), had 10 of 40 (25%) of flowers with missing anther caps. Because the anther cap and pollinia loss due to flower aging could not be distinguished from removal by *C. nitida,* male reproduction (pollinia removal rates) could not be confidently assessed.

No fruit formation was seen in any of the 11 bagged inflorescences, nor on any of the seven inflorescences on the plant held inside the screen enclosure, indicating that the plants were not apomictic or self pollinating.

The end of the bloom reproductive assessment of the three large plants indicated that they had produced 13, 26 and 57 inflorescences and a total of 876, 1241, and 5160 flowers, respectively, and a mean of 2425 flowers per plant. The three plants produced 12, 26 and 28 capsules and a mean of 22 per plant, and a mean of almost one capsule per inflorescence (0.927, SD = 0.438). A total of 66 capsules were produced overall by the 7,277 flowers, yielding effective pollination rates ranging from one half of a percent (0.54%) to a high of almost three percent (2.97%), and a mean fruit set for the three plants of almost one and half percent (1.49%, SD = 0.0129).

Discussion

The anther caps appear to be routinely shed as the flowers age, resulting in their absence in most old flowers. Fallen pollinia were frequently found on or near stigmas and also appear to be part of the aging process in the flowers. The complete absence of fruit in the bagged inflorescences and in the plant held in the screen house demonstrated that neither self pollination nor apomixis was occurring. If either had occurred, some fruit should have been produced by the enclosed inflorescences because the fruit production rate (almost one per inflorescence in the exposed plants) should have been detectible. Self pollination is known in some *Oncidium* species and occurs because the stipe of the pollinia which is standing erect initially grows outward and then downward until the pollinia contact the stigmatic surface (van der Pijl & Dodson 1969). *Oncidium sphacelatum* has been reported to be self incompatible (East 1940), which makes self pollination impossible.

The only observed visitors other than *C. nitida* was a single honey bee which did not remove a pollinarium from the single flower it visited, and two *Euglossa viridissima* which examined but did not enter flowers. Euglossine bees are not known to be associated with *Oncidium* orchids, and the rewardless flowers would be of little interest to honey bees. Southern Florida's native *C. errans* Smith is a potential visitor of *O. sphacelatum.* A single female *C. errans* was observed collecting oil from *B. lucida* at the Ft. Lauderdale study site, north of where it has been previously recorded (Pemberton & Liu 2008). *Trigona* and *Tetrapedia* species, the other known pollinators of *Oncidium* species, are tropical American bees not known to occur in Florida (http://www.discoverlife.org). Direct observation of *C. nitida* removing a pollinarium from an *O. sphacelatum* flower, and the capture of a *C. nitida* carrying an *O. sphacelatum* pollinarium indicate that this naturalized bee is pollinating this ornamental orchid in Florida. An insect carrying a pollinarium is very likely to be a pollinator of the species that produced the pollinarium (Dressler 1976). The large numbers of fruit being produced on the observed plants and the apparent absence of other pollinators also support this finding.

Among the *Centris-Oncidium* visitation syndromes reported are male bees that attack and pollinate flowers as part of its territorial defense (van der Cingel 2001), and female bees searching for food. Both of the observed *O. sphacelatum* pollinia-carrying *C. nitida* bees in this study were females that were seeking food when they visited the flowers. A few *Oncidium* species have true reward flowers, offering oil rewards (Whitten et al. 2000), but the majority employ oil deceit flowers in which the lip calli suggest the presence of oil. These *Oncidium* are thought to mimic the oil reward flowers of the many species of Malpighiaceae, which can have similar ultraviolet light patterns on their flowers (Nierenberg 1972). A recent study (Reis et al. 2007) has shown that the oil chemistry of the oil rewards of *Oncidium* species is similar to those of *Brysonima* spp. (Malpighiaceae) and that bees not only collect oils from both plants, but chemically modify the oils for use in their brood provisions.

Oncidium sphacelatum appears to be a rewardless mimic of Malpighiaceae oil reward models which exploits *C. nitida*'s oil collecting behavior. *Byrsonima lucida* is a novel model encountered by *C. nitida* in its invasive range. This native Florida shrub is the principal oil resource whose flowers are continually foraged during their entire blooming period by female *C. nitida.* The flowering periods of both plants overlap enabling the association to be reinforced on a daily basis. It is interesting to note that no fruit were observed on the *O. sphacelatum* plants prior to 2006 after a single flowering *B. lucida* was planted in the yard. As soon as this *B. lucida* shrub flowered, *C. nitida* appeared and began to regularly collect oil from the flowers. Fruit set in mimetic orchids can increase when its model is more abundant (Anderson et al. 2005). *Centris nitida* also collects oils from ornamental species of Malpighiaceae in southern Florida including *Malphighia* spp. and *Galphimia gracilis* Bartl., as well as *Angelonia angustifolia* Benth. (Scrophulariaceae).

The degree of visitation and fruit set observed in the pollination of the ornamental *O. sphacelatum* plants by the naturalized *C. nitida* in Florida is higher than seen in the recently reported pollination study of *O. sphacelatum* at two Chiapas, Mexico sites by different *Centris* species (Damon & Cruz-Lopez 2007). Three candidate bee pollinators of this orchid in the Mexican study were observed. *Centris trigonoides* Lepelier was seen to visit and continually hover before and occasionally "lunge" at the flowers at one site, exhibiting what was probably male territorial behavior. An unidentified bee was also observed to attack the flowers at both sites. Neither bee was observed to remove or deposit pollinia, but there was a modest level of fruit set (0.25%) in the 14 inflorescences at the other site, but none at the other site which had eight inflorescences. Another *Centris, C. mexicana* Smith, was observed to make brief, once-a-day visits to a few flowers at the site with eight inflorescences. This bee flew directly to the center of flowers

much as *C. nitida* can do in Florida. No pollinaria removal or deposition was observed, but *C. mexicana* was collected from an orchid garden in another Chiapas location with an *O. sphacelatum* pollinarium attached to its face, demonstrating that it can be a pollinator of this orchid. It appears that *O. sphacelatum* attracts a range of *Centris* species, which are either females seeking food or males defending their territories. Because both *C. nitida* and *O. sphacelatum* are native to Mexico and Central America, this bee, along with other *Centris* species, could be part of the same pollination web with *O. sphacelatum* and perhaps other *Oncidium* species.

Other studies of *Oncidium* species have also reported low fruit set. Fruits are rarely observed in the field for *O. hookeri* Rolfe and other Brazilian *Oncidium* species (Alcantara et al. 2006). Tremblay et al. (2005) summarized the fruit set rates for three other *Oncidium* species as 1.8%, 2.0% and 4.9%, many times higher than that recorded in *O. sphacelatum* in Mexico (0.0% and 0.25%), but not so different from the 1.49% mean fruit set I recorded in Florida. Deception orchids can have quite low visitation rates (Neiland & Wilcock 1998, Tremblay et al. 2005). Dodson reported sitting for days in Ecuador observing a flowering *Oncidium planilabre* Lindl. and saw little except for a single brief visit by a single *Centris* bee which pollinated many flowers (Dodson 1962).

The number of capsules produced on the three Florida *O. sphacelatum* plants was large (66). The number of seed produced in the capsules of *O. sphacelatum* is unknown, but probably numbers more than a million per capsule. Such a large amount of seed production in an ornamental plant increases the chances of its naturalization. One third of Florida's flora is comprised of non-native species (calculated from Wunderlin & Hansen 2003), but few orchids have naturalized. The need for mycorrhizae and specialist pollinators probably limits their naturalization (Daehler 1998). Whether or not appropriate mycorrhizae are present for *O. sphacelatum* will determine whether or not the species naturalizes in southern Florida, because it now has a specialist pollinator and appears well-suited to the normal weather conditions. However, this epiphytic species may not be able to survive the periodic hard freezes, although some native epiphytic orchids, such as *Encyclia tampense* (Lindl.) Small, apparently do.

Centris nitida might interact with other Oncidiinae orchids including the Florida native *Oncidium ensatum* Lindl., *Tolumnia bahamensis* (Nash ex Britton & Millsp.) Braem, and *Trichocentrum undulatum* (Sw.) Ackerman and M.W. Chase, all of which are rare (Wunderlin & Hansen 2003). The bee could pollinate and increase fruit production in these plants and aid their restoration. *Centris nitida* could also interact with southern Florida's native *C. errans* Fox and influence its performance as a pollinator (Pemberton & Liu 2008).

Centris nitida is the second solitary bee to recently naturalize in southern Florida. Another Mesoamerican bee, *Euglossa viridissima* Friese, was detected in 2003 and has become locally abundant (Skov & Wiley 2005, Pemberton & Wheeler 2006). Florida has none of the male orchid bee's perfume orchid mutualists, but females of this orchid bee are pollinating the ornamental orchid *Guarianthe skinneri* (Bateman) Dressler and W.E. Higgins (Pemberton 2007b). *Euglossa viridissima* also has the potential to interact with other orchids (Pemberton 2007a). The orchid bee is pollinating the newly naturalized resin-reward flower, *Dalechampia scandens* L. (Euphorbiaceae) (Pemberton & Liu in press [a]), as well as other selected native, ornamental and naturalized plants (Pemberton & Wheeler 2006). *Centris nitida* is interacting with *Cyrtopodium* orchids in southern Florida (Liu & Pemberton in press [b]). Both of these bee species and most of these plants are from tropical America. Subtropical Florida has had many tropical American plants as pre-Colombian colonizers, more recent invaders, and ornamentals. Now highly specialized solitary bees have arrived from tropical America to establish, or probably re-establish pollination mutualisms with these plants. Although these interactions make our gardens and parks much more interesting and could promote fruit production of some rare native plants, they threaten to increase the number of plant naturalizations and invasions, as well as the complexity and severity of invasive species problems.

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