Piercing of nectarless Hemerocallis (Xanthorrhoeaceae) flowers by Xylocopa varipuncta and X. virginica virginica (Apidae)

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Abstract

The native carpenter bee Xylocopa varipuncta frequently made and re-used piercings in tubular corolla bases of nonnative, nectarless Hemerocallis 'Stella de Oro' (Stella de Oro Daylily, HSDO) in the César E. Chávez Memorial Plaza in downtown Sacramento, California. The bees frequently visited HSDO flowers from mid-morning through late afternoon in August 2014 during the 3-yr, severe California drought. Their foraging bouts were up to 10 floral visits, and they were evidently obtaining cell fluid. Nonnative Apis mellifera extended their proboscides through the piercings, acting as secondary cell-fluid robbers. They also may have pollinated HSDO when they collected its pollen. Hemerocallis-flower piercing by native X. virginica virginica is apparently rare, but in the Wehawken Nature Preserve in Bethesda, Maryland, a female pierced succulent, nectarless flowers of two other Hemerocallis cultivars and three unnamed seedlings, possibly obtaining cell-fluid, learning that the flowers did not have nectar, or both during the wet summer of 2015.

Keywords

Apis, Hemerocallis, Xylocopa, cell-fluid consumption, flower-piercing
Introduction

Some species of ants, bumble bees, carpenter bees, flowerpiercer birds, hummingbirds, mammals, stingless bees, and wasps are primary nectar robbers which make holes, piercings, and slits in floral corolla tubes through which they and secondary nectar robbers, which do not make such openings, imbibe nectar (Barrows 1980; Barrows et al. 2013). These robbers cannot reach nectar in long-corolla bases because their tongues are too short. *Xylocopa* pierces flowers using its bladelike galeae, and some *Bombus* species and a vespid-wasp species chew holes into flowers with their mandibles (Schremmer 1972, Michener 2007, Barrows et al. 2013, pers. obs.). Nectar robbing can increase, reduce, or have no significant effect on plant fitness, depending on environmental factors and plant species (Maloof and Inouye 2000).

In contrast, two *Xylocopa*-bee species pierce succulent corollas of nectarless *Hemerocallis* flowers with their proboscides. The main aim of this study is to describe the frequent flower piercing of such flowers by female *X. varipuncta* (Valley Carpenter Bee), proboscis probing of these piercings by workers of *Apis mellifera* (Western Honey Bee) in California, and rare piercing of such flowers by *X. virginica virginica* (Eastern Carpenter Bee) in Maryland. This study involves two native and one nonnative bee species and hybrid plants of nonnative parentage in an urban and suburban ecosystem, respectively. *Xylocopa varipuncta* evidently imbibed cell fluid, not nectar, from the nectarless flowers. To my knowledge, this is the first report regarding frequent nectarless-flower piercing and apparent cell-fluid feeding by bees.

Methods

Study sites

I observed *A. mellifera*, *X. varipuncta*, and *H. ‘Stella de Oro’* (Stella de Oro Daylily, HSDO) on 11–15 August 2014 in the César E. Chávez Memorial Plaza in downtown Sacramento, California (Fig. 1) during the dry season of a 3-year extreme drought. All observation days were warm and sunny. The Plaza had four heavily mulched, automatically-watered HSDO beds: the north (38 clumps of HSDO shoots), north-northeast (44), south (53), and south-southwest (65) bed. There was no standing water in the fountain, or other place in the Plaza, which hymenopterans and other animals could drink. I also observed rare, daylily floral piercing by an unworn female *X. virginica virginica* on the warm, sunny day of 7 July 2015 during a wet summer in the Wehawken Nature Preserve in Bethesda, Maryland. The Preserve is within a residential neighborhood with many plant species, including large trees, and it contains about 600 cultivars and unnamed seedlings of *Hemerocallis* and several kinds of flowering plants used as nectar sources by this bee species. The focal bee was easily observed close up because she visited potted daylilies on two plant tables at about 30 cm above the ground.
Bees

The only bee species I saw in the Plaza were *A. mellifera* and *X. varipuncta*. Many apid, colletid, halictid, and megachilid bee species occur in the Preserve. The native North American *X. varipuncta* occurs from Arizona, California, and Nevada through Baja California, and the native *X. virginica* occurs from southern Canada through Florida and west through Nebraska, Kansas, Oklahoma, and Texas (Krombein et al. 1979, Powell and Hogue 1980). *Apis mellifera* is an Old World species introduced into other parts of the world, including North America. All three of these species imbibe nectar from many plant species.

Hemerocallis

*Hemerocallis* is an insect-pollinated, Eurasian monocot genus with about 15 species, 80,000 registered cultivars, and thousands of unregistered hybrids derived from the species (American Hemerocallis Society 2015). These *Hemerocallis* occur in urban and other gardens worldwide, and some species, cultivars, and unregistered clones are nec-
tar and pollen sources of both pollinators and nonpollinators (Hirota et al. 2012, Billingslea 2015, pers. obs.). In general, each flower lasts only about 24 hr, whether or not it is pollinated. Hemerocallis flowers are succulent, and cell fluid appears at freshly cut tissue of their corollas (pers. obs.). In smaller-flowering kinds of Hemerocallis, which are the subjects of this study, corolla-tube walls are 1–1.5 mm thick.

The only kind of Hemerocallis I saw in and within 650 m of the Plaza was HSDO. In the Plaza, this daylily bloomed profusely, and its 200 clumps each had all or a combination of old, brown scapes with fallen capsules; scapes with green and ripe capsules; scapes with flower buds and flowers; and small, developing scapes with flower buds. In Maryland this same cultivar has a spring and summer flush of flowers, not the continuous bloom in the Plaza. Twenty Preserve HSDO flowers were 77 ± 4.9 SD (70–85) mm long and had corolla tubes 23.6 ± 0.9 SD (21–25) mm long. Preserve non-HSDO Hemerocallis flowers visited by the X. v. virginica were larger and longer than HSDO flowers.

In 2014–2015, the Preserve had about 600 Hemerocallis cultivars and seedings, frequent visits from A. mellifera from three hives, about 30 m away, to other flowering-plant genera, and frequent Hemerocallis pollen collection by Lasioglossum bees. I measured piercing lengths in Plaza HSDO flowers with a mm rule. In looking for Hemerocallis nectar, I cut flowers from both study sites lengthwise and searched for nectar droplets, films, or both inside flowers using a magnification of 10×.

**Flower-piercing frequency**

To determine how the frequency of floral-piercing by X. varipuncta changed during a day, I sampled 193 new flowers in all four of the Plaza’s beds in the morning (10:30–11:30 a.m.) and afternoon (4:30–5:30 p.m.) on 13 August 2014. I sampled all 43 flowers in the north bed and 50 flowers in each of the other three beds, which had up to 75 flowers per bed.

**Results**

Scores of new HSDO flowers were present in the Plaza, and X. varipuncta females pierced these flowers on all observation days. In late mornings and afternoons, they quickly flew about and landed on HSDO flowers, up to 10 flowers per foraging bout in a particular bed, and probed old and new piercings with their proboscides (Fig. 2). These bees landed on flowers in three ways: (1a) a bee landed on a flower tepal and then quickly crawled down into its base, (1b) backed out, (1c) crawled to the apical area of a tepal, (1d) crawled to the outside of a flower’s floral tube, (1e) made a new piercing with her tongue or (1f) extended her tongue into a previously-made piercing; (2) a bee landed on a tepal facing away from a flower’s center and then exhibited steps 1d–1f; and (3) a bee directly landed on a floral tube and exhibited steps 1e–1f. Piercings were 1.5 mm long. During one sampling day in California, floral-piercing frequency
Piercing of nectarless Hemerocallis (Xanthorrhoeaceae) flowers by Xylocopa varipuncta...

Figure 2. A female Xylocopa varipuncta that fed on cell fluid of a Hemerocallis ‘Stella de Oro’ flower through a piercing in the flower’s corolla tube.

Table 1. Percent pierced flowers and piercing number per flower. Flowers are those of Hemerocallis ‘Stella de Oro’ pierced by Xylocopa varipuncta on 13 August 2014 in the César E. Chávez Memorial Plaza, Sacramento, California.

<table>
<thead>
<tr>
<th>Flower bed</th>
<th>Percent of flowers pierced†</th>
<th>Number flowers with 1 or 2 piercings‡</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Morning (10:30–11:30 a.m.)</td>
<td>Afternoon (4:30–5:30 p.m.)</td>
</tr>
<tr>
<td>North</td>
<td>28</td>
<td>49</td>
</tr>
<tr>
<td>North-northeast</td>
<td>0</td>
<td>26</td>
</tr>
<tr>
<td>South</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>South-southwest</td>
<td>0</td>
<td>10</td>
</tr>
</tbody>
</table>

† N = 43 flowers in the north bed and 50 flowers for the other three beds totaling 193 flowers.
‡ 12 (1) = 12 flowers with 1 piercing; 3(2) = 3 flowers with two piercings; etc.

increased from 15%–25% of 193 flowers (Table 1). Forty-one of the flowers had one piercing, and seven had two piercings by 5:30 p.m. I did not see X. varipuncta’s visiting the four other flowering species in the Plaza.

Apis mellifera workers showed two kinds of landings on HSDO flowers. In landing type-1, a worker landed on a tepal and then crawled into a flower’s throat, presumably
Figure 3. An *Apis mellifera* worker on the corolla tube of *Hemerocallis* ‘Stella de Oro’. Such bees extend their proboscides through piercings made by *Xylocopa varipuncta*.

Figure 4. An *Apis mellifera* worker that was collecting pollen of *Hemerocallis* ‘Stella de Oro’.
in search of nectar. In landing type-2, a worker landed on the top of a tepal and then crawled to the outside of its flower where she probed an already-made piercing with her proboscis (Fig. 3). *Apis mellifera* workers also landed on anthers where they collected pollen (Fig. 4). Besides visiting HSDO flowers, *A. mellifera* visited flowers of *Rosmarinus officinalis* (Rosemary) in the Plaza. Elsewhere near the Plaza, *A. mellifera* visited flowers of both *Rosmarinus officinalis* (Rosemary) and a *Zinnia* cv.

Small ants were on corollas of three HSDO flowers, but were not seen entering corollas through piercings. A male *Colias* butterfly entered four HSDO flowers through their natural corolla openings, evidently looking for nectar, and did not extend his proboscis through piercings.

In Maryland, the female *X. v. virginica* first searched the inside of a flower of *H. ‘Violacea’* and did not pierce the flower (Fig. 5). She then visited and pierced a flower of each of three unnamed seedlings (Fig. 6) and a flower of *H. ‘Brown Witch’* before she left the *Hemerocallis* patch. She spent only a few seconds at each flower. I found no evidence of nectar in the flowers when I dissected them within 10 min after her visit.

**Discussion**

*Xylocopa varipuncta* frequently pierced HSDO flowers, and individuals often flew to many of these flowers during single foraging bouts. Their frequent visits and floral piercing indicate that they were obtaining cell fluid from the nectarless flowers. It is unclear whether the bees were seeking water alone, cell contents in general, or both when they pierced the flowers. In the Plaza, *A. mellifera* that extended their tongues into previously-made piercings likely obtained cell-fluid. The female *X. v. virginica* pierced four *Hemerocallis* flowers and then flew off. She seemed to have learned that the flowers did not have nectar, obtained enough cell fluid during her piercing bout, or both. In Maryland, unworn adult butterflies, *e.g.*, *Papilio glaucus* and *P. troilus*, also visit different kinds of *Hemerocallis* flowers, and after visiting only a few flowers and likely finding no nectar, these butterflies leave *Hemerocallis* patches, evidently learning these flowers are not nectar sources (pers. obs.). However, butterflies and moths obtained nectar from two *Hemerocallis* species and their F1 and F2 hybrids in Japan (Hirotta et al. 2012).

Although I have observed many insect species on thousands of kinds of *Hemerocallis* flowers since 1976 in seven U.S. states and Japan, I saw flower piercing only by *X. varipuncta* and *X. v. virginica*. This piercing was frequent in the California site and rare in the Maryland site. There, *X. v. virginica* often hovered over *Hemerocallis* flowers and sometimes rested on their tepals and anthers, but so far, I have seen only one individual pierce such flowers.

I have seen many workers of *A. mellifera* fly about *Hemerocallis* flowers, but have never seen this bee collect *Hemerocallis* pollen outside of California. In Eastern U.S., *Lasioglossum* bees are frequent *Hemerocallis* pollen foragers that are likely *Hemerocallis* pollinators. The California HSDO plants frequently produced fruit containing seeds,
Figure 5. A female *Xylocopa virginica virginica* that entered a flower of *Hemerocallis* 'Violacea'.

Figure 6. The same female *Xylocopa virginica virginica* which pierced a corolla base of an unnamed *Hemerocallis* hybrid.
which sprouted in flower pots (pers. obs.). *Apis mellifera* may have been a key pollinator of these plants.

The long California drought and dearth of nectar in Sacramento may have favored daylily floral-piercing and cell-fluid imbibing by *X. varipuncta*. It would be interesting to determine if these bees visit HSDO flowers during times of abundant nectar in flowers of other species used by this species. Determination of this was not possible in 2015, because the Sacramento area was in its fourth year of extreme drought. In the Maryland case, a young female *X. v. virginica* evidently quickly learned that daylilies she visited did not have nectar. She may have imbibed cell-fluid although water was often on plants and in shallow plant trays in the Preserve, and nectar was available in other flowers. Although I have seen *X. v. virginica* fly over, land, and rest on daylily flowers scores of times, this was the only case of *Xylocopa Hemerocallis* piercing that I have seen in Eastern U.S. I have seen *A. mellifera*, but not *X. v. virginica*, drink water in the Preserve.

In conclusion, the California *X. varipuncta* behaved as if they were primary cell-fluid robbers, and *A. mellifera* behaved as if they were secondary cell-fluid robbers. The Maryland *X. v. virginica* exhibited one foraging bout during which she likely learned that *Hemerocallis* flowers she visited did not have nectar, obtained an adequate amount of cell fluid, or both. Given the high abundances of many kinds of *Hemerocallis* in gardens, parks, and rural areas in many parts of the world; the hundreds of *Xylocopa* spp.; and the cosmopolitan distribution of *A. mellifera*; there should be many other cases of *Apis-Hemerocallis-Xylocopa* interactions awaiting discovery.

**Acknowledgments**

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**References**


