Parasitism of *Dasineura oxycoccana* (Diptera: Cecidomyiidae) in North Central Florida

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ABSTRACT   Blueberry gall midge, *Dasineura oxycoccana* (Johnson), is a key pest of blueberries in Florida. As a larva, this insect feeds in developing flower and leaf buds. Management of *D. oxycoccana* relies principally on chemical insecticides; however, efficacy is limited because *D. oxycoccana* is sheltered within the plant during most of its life cycle. Natural enemies, particularly parasitoids, may play an important role in regulating *D. oxycoccana* populations. To determine the seasonal dynamics and parasitism rates of eulophid and platygastrid wasps parasitizing *D. oxycoccana* larvae, we sampled *D. oxycoccana* larvae by collecting infested blueberry leaf buds from a minimally-managed farm in north central Florida. Midge larvae were examined under a microscope to determine parasitism status of host instars. Parasitism rates ranged from 25 to 40% over the 3-yr study. Percent parasitization was significantly higher in third instars than first or second instars. Midge larvae in the centers of leaf buds were significantly less likely to be parasitized than larvae in outer layers of leaf buds. Thirty-seven percent of midge larvae had been parasitized multiple times, suggesting these parasitoids do not discriminate between parasitized and unparasitized hosts. Implications for pesticide use in relation to the conservation of natural enemies and management of *D. oxycoccana* populations are discussed.

KEY WORDS   blueberry gall midge, parasitism, *Aprostocetus*, blueberry

Blueberries, *Vaccinium* spp. (Ericaceae), are important fruit crops in North America. From 2000 to 2010 blueberry acreage in the United States increased by 72.6% and production more than doubled (USDA NASS 2011). Expansion of the blueberry industries has been influenced by the public's interest in the health benefits of *Vaccinium* fruits. Blueberries and cranberries are rich in phenolic compounds and essential nutrients known to have antioxidant and anticarcinogenic properties (Zheng and Wang 2003). Florida is one of the major producers of early-season blueberries in North America. The state's mild winters make early production possible. Southern highbush blueberries (hybrids of *Vaccinium virgatum* Aiton, *Vaccinium corymbosum* L., and *Vaccinium darrowii* Camp) grown in central Florida can be harvested in April and May, a period of low supply and high demand (Lyrene 1989).

Blueberries are attacked by a variety of arthropod pests. Although key pest status varies by region, blueberry gall midge, *Dasineura oxycoccana* (Johnson), is found almost everywhere blueberries are grown (Steck et al. 2000). *Dasineura oxycoccana* is native to eastern North America and feeds exclusively on *Vaccinium* spp. (Sampson et al. 2006). In cranberry, *D. oxycoccana* is referred to as cranberry tipworm, but recent evidence based on reproductive isolation and mitochondrial DNA analysis suggests cryptic speciation between populations from blueberry and cranberry (Cook et al. 2011, Mathur et al. 2012).

The injury caused by *D. oxycoccana* on blueberry and cranberry leaf buds has been recognized for many years, but in 1992 it was reported that it also causes serious injury to blueberry flower buds (Barnes 1948, Marucci 1977, Lyrene and Payne 1992). Before this, loss of flower buds had been erroneously attributed to freeze damage or inadequate chilling (Lyrene and Payne 1995). Females lay eggs in flower buds early in the season as bud scales begin to separate (Lyrene and Payne 1995, Dernisky et al. 2005). When the eggs hatch, larvae crawl deeper into the buds and begin feeding on the innermost meristomatic tissues, which result in necrosis and bud abortion (Sampson et al. 2002). In susceptible rabbiteye blueberry (*V. virgatum*) cultivars, *D. oxycoccana* can destroy 80–90% of the flower buds (Lyrene and Payne 1992). Later in the season, as flower buds become scarce, females begin laying eggs in leaf buds. Feeding injury to young leaves causes them to become distorted and cupped (Barnes 1948). When vegetative meristems are killed, plants produce only short shoots with a few deformed leaves (Lyrene and Payne 1995).

Chemical control is the principal strategy available for managing *D. oxycoccana*. The effectiveness of chemical control is limited, however, because the larvae feed inside the plant and are protected from most foliar insecticides (Lyrene and Payne 1995). More

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focus needs to be placed on developing alternative strategies such as biological control. Little research has been done on the natural enemies of *D. oxycoccana*, and in many parts of its geographical range the identity of its natural enemies has not yet been determined. This leaves gaps in our knowledge of *D. oxycoccana* ecology, making it difficult to devise biological control strategies for management of this pest.

Several natural enemies of *D. oxycoccana* have been cited in the literature. These include predatory hover flies (Diptera: Syrphidae) in the genus *Toxomerus* and parasitoid wasps (Hymenoptera) in the families Ceraphronidae, Eulophidae, and Platygastridae (Barnes 1948; Mahr and Kachadoorian 1990; Sampson et al. 2002, 2006). Sampson et al. (2006) collected *D. oxycoccana* larvae in Mississippi, Louisiana, and Alabama and reared out parasitoids in the following four genera: *Aprostocetus* (Eulophidae: Tetrastichinae), *Synopeas*, *Inostemma*, and *Platygaster* (Platygastridae: Platygastrinae). The species of *Aprostocetus* collected had not been described previously (Sampson et al. 2006). Two species of parasitoids, one within the genus *Aprostocetus* and one within the genus *Platygaster*, also were collected from *D. oxycoccana* infesting cranberry in British Columbia, Canada (Peach et al. 2012).

Many gall midge species are parasitized by eulophid and platygastrid wasps (MacGown and Osgood 1972, Baxendale et al. 1983, Schuster and Lidell 1990, Williams et al. 1999, Tomkins et al. 2000, Vétek et al. 2006). Parasitoids could also play an important role in regulating *D. oxycoccana* populations in Florida blueberries. Our objective was to determine the seasonal dynamics and parasitism rates of eulophid and platygastrid wasps parasitizing *D. oxycoccana* larvae infesting blueberry leaf buds.

Materials and Methods

Blueberry gall midge larvae were sampled at an organic blueberry farm in Gainesville, FL (Alachua County). This farm had been established ≈25 yr ago and grew only rabbiteye blueberries. *Dasineura oxycoccana* larvae were sampled from infested leaf buds in 2009, 2010, and 2011. Only leaf buds that appeared injured were collected. Buds were placed in 59-ml plastic cups and taken to the Small Fruit and Vegetable integrated pest management (IPM) Laboratory at the University of Florida Entomology and Nematology Department (Gainesville, FL) for dissection. Live midge larvae were placed in a drop of water on a microscope slide, compressed under a glass cover slip, and examined under a compound microscope (Olympus CX41, Olympus America, Center Valley, PA). Immature stages of parasitoids were counted in vivo.

In 2009, samples (15–20 buds) were taken on 25 February, 4 March, and 11 March to determine the onset of midge infestation. The first day on which parasitism was observed was 11 March, so sampling commenced the next week. Fifty to 60 leaf buds were collected each week from 18 March to 8 April. In 2010, 50–75 leaf buds were collected twice a week from 31 March to 28 April. In 2011, early season samples were taken weekly from 23 February to 16 March. Regular weekly sampling (60 buds per week) commenced on 23 March and concluded on 27 April. Sampling was suspended by the end of April each year because by that time most leaf buds had opened and *D. oxycoccana* larvae became scarce.

Bud length was measured to the nearest 0.1 mm before dissection by using calipers. Leaf buds had three layers in which midge larvae could be found; therefore, the number of host larvae, host instars, and the number of parasitoids (eggs and larvae) were recorded for each leaf bud layer. Percent parasitism was calculated using the following formula: % parasitism = $P/(M + P) \times 100$, where P is the number of parasitized larvae in a sample and M is the number of unparasitized larvae (Sampson et al. 2002). Data are reported on a per leaf bud basis.

Statistical Analysis. Differences in mean percent parasitism by host instar and host location (leaf bud layer) were analyzed separately using one-way analysis of variance (ANOVA) for binomial data (PROC GLIMMIX), and posthoc means separation tests were performed using the DIFF option in the LSMEANS statement (SAS Institute 2009). The effects of host instar, host location, and their interaction on the number of parasitoid immatures were analyzed using a two-way ANOVA (PROC MIXED). Data were $(x + 1)^{-2}$ transformed to correct for normality. Degrees of freedom were adjusted using the Satterthwaite option and differences among means were determined using Tukey–Kramer procedures ($P < 0.05$) (SAS Institute 2009). The relationships between leaf bud length to the total number of hosts and the number of parasitized hosts were analyzed using PROC CORR (SAS Institute 2009). Untransformed arithmetic means are reported in figures and tables.

Results

Dasineura oxycoccana larvae dissected from leaf buds contained parasitoid immatures: oblong ovoid eggs visible within the host midgut and cyclopoid larva visible in the host hemocoel. Only 1.5, 5.9, and 1.2% of infested midge larvae contained cyclopoid larvae in 2009, 2010, and 2011, respectively. Leaf bud collection data are summarized in Table 1. The number of *D. oxycoccana* larvae examined each year varied, but there were no significant differences in the mean number of larvae per leaf bud ($F = 0.52$; df = 2, 1287; $P = 0.595$) or the mean number of parasitoid immatures per parasitized larva ($F = 0.72$; df = 2, 339; $P = 0.486$). The majority of parasitized *D. oxycoccana* larvae (62.2%) were parasitized only once. Some midge larvae contained up to seven parasitoid immatures. It could not be determined if the immatures deposited in a given midge larva came from one or multiple parasitoid females.

Midge infestation and percent parasitism by date are shown in Figs. 1, 2, and 3. Highest midge densities were observed on 8 April in 2009 (Fig. 1), 9 April in 2010 (Fig. 2), and 23 March in 2011 (Fig. 3). Peaks in parasitism rates occurred 1–3 wk after peak midge

Table 1.   Details of samples collected from rabbiteye blueberry leaf buds from an organic blueberry farm in Gainesville, FL

Year	No. buds collected	No. midge larvae	Mean ± SEM larvae/bud[a]	Parasitization rate (%)	Mean ± SEM immatures/host[a,b,c]
2009	235	523	2.23 ± 0.21	37.5	1.24 ± 0.11
2010	564	1169	2.07 ± 0.18	40.4	1.18 ± 0.07
2011	489	932	1.91 ± 0.19	27.0	1.06 ± 0.11

[a] Means reported in the table are untransformed arithmetic means.
[b] Eggs and larvae of parasitoid wasps.
[c] Parasitized hosts only.

density in 2010 and 2011, but 1 wk before peak midge density in 2009.

Most *D. oxycoccana* larvae dissected from leaf buds were second instar and relatively few first instars were collected (Table 2). Percent parasitism varied significantly among host instars in 2009 ($F = 32.4$; df = 2, 180; $P < 0.001$), 2010 ($F = 42.3$; df = 2, 346; $P < 0.001$), and 2011 ($F = 23.4$; df = 2, 244; $P < 0.001$). The highest proportion parasitized were third instars followed by second instars. The mean number of parasitoid immatures per host was not significantly different among host instars in 2009 ($F = 0.52$; df = 2, 3.31; $P = 0.637$) and 2011 ($F = 2.62$; df = 1, 203; $P = 0.107$), but differences were observed in 2010 ($F = 12.8$; df = 2, 2.48; $P = 0.049$) (Table 2), where a significantly higher number of parasitoid immatures was found per third instar than second instar. There were no interactions between host instar and leaf bud layer in any year.

Blueberry leaf buds ranged from 7.1 to 27.4 mm in length (mean: 16.1 ± 0.1 mm). The number of *D. oxycoccana* in a leaf bud was positively correlated with leaf bud length (2009: $\rho = 0.183$, $P = 0.014$; 2010: $\rho = 0.201$, $P < 0.001$; 2011: $\rho = 0.359$, $P < 0.001$). There was also a positive correlation between leaf bud length and the number of parasitized *D. oxycoccana* in 2010 ($\rho = 0.236$, $P < 0.001$) and 2011 ($\rho = 0.273$, $P < 0.001$) but not in 2009 ($\rho = 0.045$, $P = 0.547$). There was a negative correlation between the number of *D. oxycoccana* larvae in a leaf bud and the number of parasitoid immatures per host (2009: $\rho = -0.184$, $P = 0.039$; 2010: $\rho = -0.154$, $P = 0.018$; 2011: $\rho = -0.212$, $P = 0.006$).

D. oxycoccana larvae were most commonly found in the outer and middle layers (Table 3). Leaf bud layer

had a significant effect on percent parasitism in 2009 ($F = 12.5$; df = 2, 200; $P < 0.001$), 2010 ($F = 6.05$; df = 2, 382; $P = 0.003$), and 2011 ($F = 3.90$; df = 2, 245; $P = 0.022$). In all cases, hosts in the outer layer had a significantly higher rate of parasitism than hosts in the inner layer. The mean number of parasitoid immatures per host was not significantly different among leaf bud layers (Table 3).

Discussion

This was the first survey of *D. oxycoccana* parasitoids conducted in rabbiteye blueberries in Florida. These parasitoids actively parasitize *D. oxycoccana* larvae infesting rabbiteye leaf buds. We hypothesized that the parasitoids belong to the species *Platygaster* and *Aprostocetus* but further work is needed to confirm the exact identity of the species. The wasps collected in Florida should be compared with those from Mississippi (Sampson et al. 2006) to determine if the species complex is the same. Sampson et al. (2006) developed a mitochondrial DNA analysis for adult parasitoids, which could make comparisons between regions faster and more reliable. In addition, wasps collected from blueberry plantings in Florida should be compared with those collected from cranberry. The parasitoids identified from British Columbia, Canada were reared from *D. oxycoccana* infesting cranberry (Peach et al. 2012), which appears to be a different species than the one infesting blueberry (Cook et al. 2011, Mathur et al. 2012).

The ovoid eggs and cyclopoid larvae observed in *D. oxycoccana* resembled species of *Aprostocetus* and
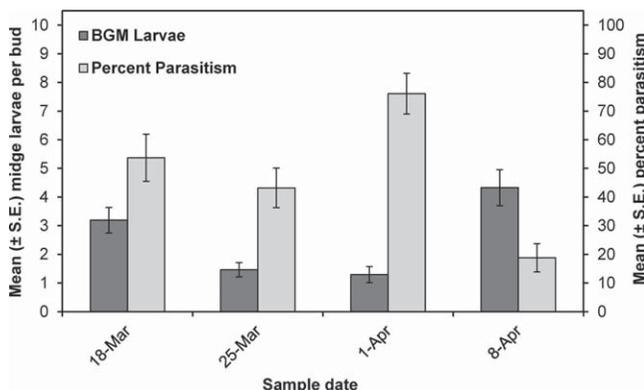
Fig. 1. Mean (±SEM) *D. oxycoccana* larvae per rabbiteye blueberry leaf bud and mean (±SEM) percent parasitism by sample date in 2009.
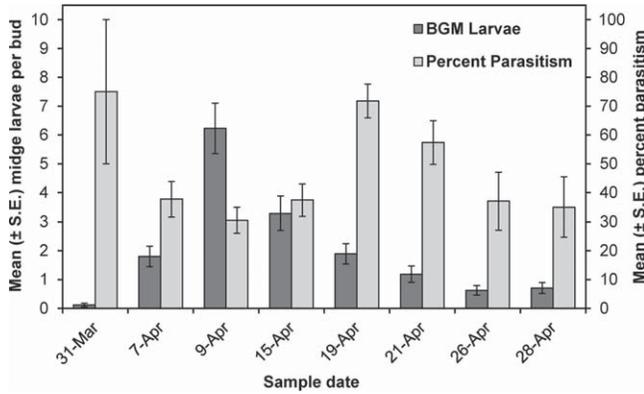
Fig. 2. Mean (±SEM) *D. oxycoccana* larvae per rabbiteye blueberry leaf bud and mean (±SEM) percent parasitism by sample date in 2010.

Platygaster as illustrated and described by Sampson et al. (2006). Unfortunately, we were unable to rear parasitoid adults for species identification because most larvae did not survive examination on the microscope slides. Larvae tended to rupture when manipulated on the slide to get an accurate count of parasitoid immatures or when attempting to remove cover slips.

Levels of parasitism were similar in Florida and Mississippi (30–40%) (Sampson et al. 2006). Percent parasitism increased with each successive host instar. Sampson et al. (2006) observed that most female *Aprostocetus* oviposited in third-instar midges. Studies on the midge *Stenodiplosis* (*Contarinia*) *sorghicola* Coquillett, parasitism showed that the parasitoid *Aprostocetus diplosidis* Crawford primarily attacked middle-stage larvae (Baxendale et al. 1983) and *A. coimbatorensis* Rohwer attacked mid- to late-stage larvae (Nwanze et al. 1998). One hypothesis for this difference is that first instars may be difficult to locate within the bud and, therefore, escape being parasitized. For example, *Aprostocetus* females walk along the length of blueberry leaf buds, probing with their ovipositor until they find a midge larva (Sampson et al. 2013). Large midge larvae would have a higher prob-

ability of being found by this apparently random ovipositor probing. Another eulophid, *Sympiesis sericeicornis* Nees, responds to vibrational cues of its leafminer host feeding within the plant (Meyhöfer et al. 1997). The fact that parasitism also varied with leaf bud layer lends support to this host apparency hypothesis with more midge larvae being parasitized closer to the leaf bud surface than near the center. For this hypothesis to be valid, female parasitoids must be able to assess host quality through ovipositor probing.

Parasitoids of gall midges tend to develop singly within each host larva (Sampson et al. 2002). It seems counterintuitive, therefore, that over 37% of parasitized midge larvae contained multiple parasitoid immatures, in some cases up to six or seven. With only one wasp able to complete development per host, this appears to be a waste of resources. Superparasitism frequently is observed in field populations even though host discrimination is a common phenomenon among parasitic wasps (Bakker et al. 1985). Therefore, our observation of superparasitism is not unusual, and there are situations in which superparasitism may be advantageous. If a parasitoid locates host habitat but most hosts have already been parasitized by conspecifics, superparasitism may be beneficial (Bakker et al.
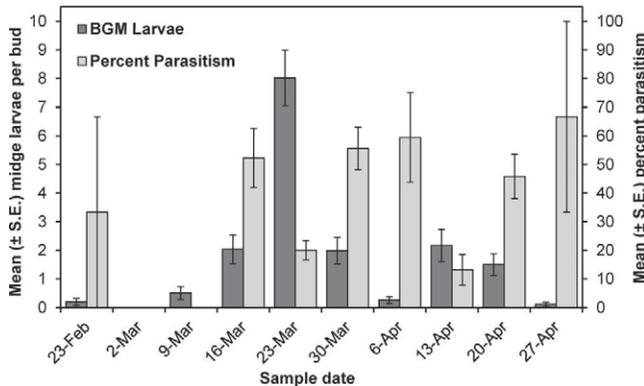

Fig. 3. Mean (±SEM) *D. oxycoccana* larvae per rabbiteye blueberry leaf bud and mean (±SEM) percent parasitism by sample date in 2011.

Table 2. Incidence of parasitism and number of parasitoid immatures per *D. oxycoccana* larva by host instar

Year	Midge instar	No. midge larvae	Mean ± SEM % parasitism[a]	Mean ± SEM immatures/host[a,b,c]
2009	First	126	7.62 ± 4.18a	1.25 ± 0.25
	Second	272	45.3 ± 4.97b	1.63 ± 0.09
	Third	125	62.9 ± 5.31c	1.79 ± 0.11
2010	First	111	6.54 ± 3.55a	1.60 ± 0.25ab
	Second	713	40.9 ± 3.10b	1.44 ± 0.05a
	Third	345	61.8 ± 3.65c	1.86 ± 0.08b
2011	First	37	2.78 ± 2.78a	–
	Second	606	26.1 ± 3.21b	1.41 ± 0.08
	Third	289	47.6 ± 4.24c	1.60 ± 0.10

Host larvae collected from rabbiteye blueberry leaf buds.
[a] Means reported in the table are untransformed arithmetic means.
[b] Eggs and larvae of parasitoid wasps.
[c] Parasitized hosts only.

1985). The energy required searching for another host habitat and suitable hosts could outweigh the risk of competition. In our data, a higher incidence of superparasitism was observed where the number of parasitized midge larvae per leaf bud was higher. It is apparent, therefore, that these parasitoids will oviposit in already parasitized midge larvae when parasitism in the host population is high. An examination of the ovipositor of *A. procerae* Risbec showed that it is equipped with many mechanoreceptive sensillae and some chemoreceptors distributed along its length (Nacro and Nénon 2009). It is likely that species of *Aprostocetus* parasitizing hosts concealed within plants use ovipositor sensillae to detect the presence of the host, but it is not clear if they can assess the status (parasitized or unparasitized) of the host. Further work needs to be done on host selection behavior of *Aprostocetus* and other parasitoids.

This survey confirmed the presence of *D. oxycoccana* parasitoids in north central Florida, but further studies need to be conducted to identify these parasitoids to species and determine their impact on *D. oxycoccana* populations over the blueberry growing season. High parasitism rates suggest that parasitoid wasps could play an important role in *D. oxycoccana*

population regulation in blueberries. In cases where insecticides must be used, applications should be carefully timed and reduced-risk insecticides used to avoid disrupting natural enemies.

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Table 3. Incidence of parasitism and number of parasitoid immatures per *D. oxycoccana* larva by leaf bud layer

Year	Leaf bud layer	No. midge larvae	Mean ± SEM % parasitism[a]	Mean ± SEM immatures/host[a,b,c]
2009	Outer	252	53.0 ± 4.55a	1.66 ± 0.09
	Middle	194	39.8 ± 5.10b	1.75 ± 0.14
	Inner	77	22.6 ± 6.32b	1.67 ± 0.27
2010	Outer	383	48.4 ± 3.77a	1.70 ± 0.09
	Middle	534	44.9 ± 3.22a	1.63 ± 0.06
	Inner	252	30.7 ± 4.22b	1.45 ± 0.09
2011	Outer	261	31.8 ± 4.82a	1.39 ± 0.09
	Middle	357	36.0 ± 3.95a	1.49 ± 0.10
	Inner	225	22.6 ± 4.18b	1.44 ± 0.13

Host larvae collected from rabbiteye blueberry leaf buds.
[a] Means reported in the table are untransformed arithmetic means.
[b] Eggs and larvae of parasitoid wasps.
[c] Parasitized hosts only.

(Hymenoptera: Platygasteridae) and *Aprostocetus procerae* (Hymenoptera: Eulophidae) two parasitoids associated with the African rice gall midge *Orseolia oryzivora* (Diptera: Cecidomyiidae). Psyche 2009: 1–7.

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