

Nectar-Robbing Carpenter Bees Reduce Seed-Setting Capability of Honey Bees (Hymenoptera: Apidae) in Rabbiteye Blueberry, *Vaccinium ashei*, 'Climax'

SELIM DEDEJ AND KEITH S. DELAPLANE

Department of Entomology, University of Georgia, Athens GA 30602

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ABSTRACT The carpenter bee, *Xylocopa virginica* (L.), acts as a primary nectar thief in southeastern plantations of native rabbiteye blueberry, *Vaccinium ashei* Reade, perforating corollae laterally to imbibe nectar. Honey bees, *Apis mellifera* L., learn to collect nectar from these perforations and thus become secondary thieves. We conducted a 2-yr study to assess how nectar robbing in honey bees affects fruit production in rabbiteye blueberry. Various harvest parameters were measured from fruit collected from plants tented with honey bees and carpenter bees (AX), carpenter bees (X), honey bees (A), no bees (0), or in open plots (open). In open plots, rates of illegitimate honey bee flower visitation increase from initial lows to fixation at $\geq 95\%$. Fruit set is higher in open, A, and AX plots than in X and 0 plots. Even though fruit set is similar in A and AX plots, seed numbers are significantly reduced in AX plots in which *X. virginica*-induced illegitimate honey bee flower visitation approaches 40%. Open-pollinated berries were larger than berries from all other treatments in 2001, whereas in 2002 berry weight followed the pattern A > open > AX > (X \approx 0). Sucrose content of juice and speed of ripening were unaffected by treatments.

KEY WORDS nectar robbing, rabbiteye blueberry, *Vaccinium ashei*, *Apis mellifera*, *Xylocopa virginica*

CARPENTER BEES, *Xylocopa* Latreille, are common flower visitors in the southeastern United States (Cane and Payne 1990; Delaplane 1995). Some flowers, including rabbiteye blueberry, *Vaccinium ashei* Reade, possess long, tubular corollae in which nectar is inaccessible to the carpenter bees, so the bees obtain nectar by imbibing it through perforations they make with their maxillary galeae in the walls of the calyx or corolla. This behavior is called nectar theft or robbery (Faegri and Van der Pijl 1979; Inouye 1980, 1983). Carpenter bees have been reported to act as nectar thieves in *P. grandiflora* Rothm. (Guitian et al. 1994); ocotillo, *F. splendens* Engelm. (Scott et al. 1993), as well as blueberry (Cane and Payne 1990, Delaplane 1995, Sampson and Cane 2000). Nectar-thieving flower visits often do not result in pollination benefit to the plant (Inouye 1980, 1983; Maloof and Inouye 2000). The removal of floral nectar by robbers decreases the standing crop and in some cases changes the sugar concentration of nectar available to other pollinators (Pleasant 1983).

In the southeastern United States, *Xylocopa virginica* (L.) (Cane and Payne 1990) and *Xylocopa micans* (Lepeletier) (Delaplane 1995) are frequent visitors to commercial blueberry orchards. Both engage in nectar thievery and are considered ineffective pollinators of this native crop species. Delaplane (1995) documented that 100% of blueberry flower visits by both species are acts of nectar thievery. Moreover, the

robbery holes in flowers made by *X. virginica* and *X. micans* are attractive to honey bees, *Apis mellifera* L., a species commonly imported for commercial pollination. Honey bees are incapable of making robbery holes, but readily visit holes made by *Xylocopa* spp. and thus act as secondary nectar thieves (Delaplane and Mayer 2000). Delaplane (1995) showed that 92.3% of honey bees were observed to rob nectar in the presence of *Xylocopa* spp.

Previous studies have documented the primary nectar-thieving activity of carpenter bees and its secondary expression by honey bees, but no information is available about the effect of these behaviors on the pollination efficacy of *A. mellifera* in rabbiteye blueberry. Honey bees are effective pollinators of *V. ashei* 'Climax' (Sampson and Cane 2000, Dedej and Delaplane 2003), but it is possible that their efficacy is compromised when they are diverted to robbing behavior. Hence, we designed a 2-yr study to compare incidence of honey bee robbing behavior, fruit set, seed number, berry weight, sucrose content of juice, and speed of ripening in rabbiteye blueberry plants tented with various combinations of *A. mellifera* and *X. virginica*.

Materials and Methods

Orchard and Experimental Setup. The study was conducted at a permanent orchard at the Horticulture Farm of the University of Georgia, Oconee County,

Georgia, in 2001 and 2002. Mature rabbiteye blueberry (*V. ashei*) plants in alternating rows of 'Climax' and 'Premier' were used. The experiment consisted of caging plants during the bloom period with standardized densities of honey bees and carpenter bees, recording flower visitation behavior of honey bees during bloom, and measuring characteristics of fruit at harvest. Overhead irrigation was used to prevent frost damage to flowers (Eck 1988) when ambient temperatures reached -2°C (1–2 nights per year). Drought conditions prevailed in 2001–2002, and when farm managers deemed it necessary the whole orchard would be irrigated.

Treatments and Bees. Treatments consisted of plots, each with two homogeneous mature 'Climax' plants (15-yr old, 1.6–1.8 m) that were either tented with bees or left open as controls. Tents were 1.8 by 1.8 by 1.8-m units covered with Lumite screen (Bioquip Corp., Gardena, CA). Tented plots were provided two vigorously flowering 3-gal potted 'Premier' as pollenizers, whereas open plots were not provided potted pollenizers because of the ambient abundance of 'Premier'. We supplemented the potted pollenizers with fresh cuttings of flowering 'Premier' after potted pollenizers exceeded 50% flower drop. Five treatments were organized as follows: 1) honey bees and two carpenter bees combined in one tent (*Apis/Xylocopa*, AX), 2) two carpenter bees (*Xylocopa*, X), 3) honey bees (*Apis*, A), 4) no bees (0), and 5) open plot (open). Treatments were assigned randomly to tents, and there were two tents per treatment in 2002 and one per treatment in 2001. Because the university research apiary is near the experimental orchard, honey bees, as well as other bee species, were able to visit the open plots freely. Standard densities of 3,200 honey bees [initial counts, determined after Delaplane and Hood (1997)] and two carpenter bees per tent were used. The density of 3,200 honey bees was chosen because there is evidence that under identical conditions this density is nonlimiting in either performance of pollinators or availability of pollenizer pollen (Dedej and Delaplane 2003). The number of two carpenter bees per tent was considered a reasonable compromise between inefficacy (risk of no flower perforations) and satiation (completely perforated); this was shown to be a good choice as the rates of perforated flowers in the AX plots ranged from 0 to 50% (23.2 ± 2.9 , $n = 60$) over the 2 yr of study. Second, the effects of *X. virginica* on honey bees are profound at what seem to be low densities; as few as one carpenter bee per 25 bushes, or 4% incidence of punctured corollae, can divert 80–90% of honey bees to robbing behavior (Cane and Payne 1991). And finally, our unpublished observations indicate a natural ambient visitation rate by *X. virginica* per two bushes in this orchard to be 2.3 ± 1.6 ($n = 19$) visits per 2 min.

Honey bees were added to the plots (22 March 2001 and 24 March 2002) when advanced buds were at stage five (Spiers 1978). Colonies were fed regularly with sugar syrup and socially stabilized with synthetic queen mandibular pheromone (QMP) (one queen equivalent of Bee-Boost) (Currie et al. 1994). QMP

was used in lieu of a queen to eliminate confounding effects of differential brood production resulting from variable bee populations.

Carpenter bees were caught and added to the appropriate tents as soon as they were naturally available. They were checked every day and if missing or dead substituted with fresh ones, always maintaining two *X. virginica* per tent. Carpenter bees were replaced with fresh ones after being used for 1 wk. We used exclusively male carpenter bees as they are the first active in a season and occur in near-synchrony with the onset of *V. ashei* flowering. The inclusive dates during which *X. virginica* were present in experimental tents were 2–23 April 2001 and 28 March–18 April 2002. Wooden blocks (4 by 8 by 6 cm) each with a 1-cm-diam. hole were provided to tents, and carpenter bees were occasionally observed to use them as shelters.

Dependent Variables. At stages 4–5 of blooming (Spiers 1978), the number of unopened flowers per raceme was determined for 40 tagged racemes distributed approximately equally between the two 'Climax' plants in each plot; this was done on 19–20 March 2001 and on 22–23 March 2002 before inserting bees into tents. To compensate for wind loss of tags, twice as many racemes (80) were marked in the open plots.

On 14–15 d during the bloom period (2–23 April 2001 and 28 March–17 April 2002), we measured for each plot (excluding the non-*Apis* tents 0 and X) the proportion of illegitimate honey bee flower visits (based on number of visits per 2 min) during normal flight hours (1100–1600 hours). Visits during which honey bees probe the terminal aperture of the flower, presumably effecting pollination, were considered legitimate (L), whereas those realized by probing lateral robbery holes made by carpenter bees were considered illegitimate (I) (Faegri and Van der Pijl 1979). The average percentage of honey bee flower visits illegitimate was calculated for A, AX, and open plots as $(I + (L + I)) \times 100$. Data from open plots were subsequently used to make asymptotic models testing various relationships among dependent variables (see below).

To monitor the condition of flowers under ambient orchard conditions, we measured in the open plots on 9, 16, and 23 April 2001 and 4 and 11 April 2002 the percentage of open flowers with lateral perforations in their corollae, calculated as (perforated open flowers + (perforated open + nonperforated open)) $\times 100$. These measurements were made for each of 10 racemes per open plot per sampling day ($n = 70$).

After bloom was finished, all bees were removed and the Lumite screens replaced with poultry netting to protect fruit from animals and unauthorized harvesting.

Percentage fruit set ([no. fully formed fruit \div no. unopened flowers] $\times 100$) was determined for each recovered raceme while fruit were full-sized but still green. Harvest of ripe fruit was done from 16 June to 15 July 2001 and from 12 June to 15 July 2002. The following dependent variables were measured for each recovered raceme: percentage of fruit set, number of

Table 1. Rates of illegitimate honey bee visitation and fruit characteristics (% fruit set, sucrose content, and speed of ripening) of 'Climax' rabbiteye blueberry as affected by honey bees and carpenter bees in tents (≈ 2 by 2 m)

Treatment	% Illegitimate <i>A. mellifera</i> visits	% Fruit set	% Sucrose content of juice	Speed of ripening
Open	90.1 \pm 3.5a (38)	59.9 \pm 2.4a (198)	13.7 \pm 0.24a (112)	46.8 \pm 2.8a (158)
A	0c (36)	71.3 \pm 2.6a (115)	13.9 \pm 0.3a (103)	41.2 \pm 3.3a (90)
AX	39.4 \pm 6.0b (36)	73.6 \pm 2.2a (113)	13.8 \pm 0.3a (97)	19.8 \pm 2.5a (110)
X	NA	21.9 \pm 2.3b (110)	15.5 \pm 0.3a (63)	23.4 \pm 4.0a (64)
0	NA	25.1 \pm 2.7b (110)	16.0 \pm 0.3a (56)	26.1 \pm 4.6a (64)

Speed of ripening was calculated as the proportion of fruits ripe per raceme on two arbitrarily chosen dates when fruit was 30–50% ripe. Five treatments were organized as follows: 3,200 honey bees and two carpenter bees combined in one tent (*Apis/Xylocopa*, AX), two carpenter bees (*Xylocopa*, X), honey bees (*Apis*, A), no bees (0), and open plot (open). Data are pooled for years 2001 and 2002. Values are mean \pm standard error, with *n* in parentheses. Means within a column followed by the same letter are not significantly different at the $\alpha = 0.05$ level. NA, not applicable.

seeds per fruit, berry weight (grams), speed of ripening, and sucrose content of juice. Number of seeds per fruit was determined by expressing berry contents and counting the number of apparently viable seeds (Lyrene 1989, MacKenzie 1997, Ritzinger and Lyrene 1998) as discriminated by a single observer. Speed of ripening was calculated as the proportion of fruits ripe per raceme on two arbitrarily chosen dates, 15 June 2001 and 1 June 2002, when fruit was 30–50% ripe. Fruit juice was collected by piercing each sampled berry with a microcapillary tube, and percentage of sucrose content of juice determined with a bench-top refractometer (Fisher Scientific Co., Pittsburgh, PA). Data for parameters requiring destructive sampling of ripe fruit (number of seeds, berry weight, and sucrose content of juice) were collected sequentially as ripe fruit became available. Fruit weight and sucrose content data were collected within 2 h of harvest; seed counts were sometimes delayed until the next day.

Statistical Analyses. The effects of year and treatment on incidence of illegitimate honey bee visits, fruit set, number of seeds per fruit, berry weight, speed of ripening, and sucrose content of juice were tested with a randomized design analysis of variance (ANOVA) recognizing tent (year \times treatment) as error term and testing for interactions of treatment with year. When treatment and year interacted, we analyzed independent variables by year and used residual error as test term. Means were separated by Duncan's test and differences accepted at the $\alpha \leq 0.05$ level (SAS Institute 1992).

The relationships between honey bee robbing behavior (*y*) and time (*x* in Julian days) under ambient orchard conditions (open tents) and honey bee robbing behavior (*y*) and percentage flowers perforated (*x*) were described using the Mitscherlich asymptotic growth model (Ware et al. 1982) and the NLIN procedure (SAS Institute 1992). The model was $y = \beta (1 - pe^{-\alpha(x - x_p)})$ where β is maximum asymptotic value of *y* as *x* approaches ∞ , *e* is exponential function, α is constant of proportionality, and x_p is the value of *x* where *y* reaches $1 - p$ of β . In our case, β was restricted to ≤ 100 , and *p* was set to 0.05, which solved the value of x_p with 0.95 of β .

Results and Discussion

Honey Bee Foraging Behavior on *V. ashei* and Condition of Flowers. The percentage of honey bee flower visits illegitimate in open, A, and AX plots was affected by treatment ($F = 1048.3$; $df = 2, 3$; $P < 0.0001$); there were no year effects or interactions of treatment with year ($F \leq 4.8$; $df = 1$ or $2, 3$; $P \geq 0.1153$). The mean separations in Table 1 indicate that differences were wholly explained by the co-occurrence of honey bees with *X. virginica*. Nectar thievery by honey bees was highest in open plots followed by AX tents but non-existent in the A tents from which *X. virginica* were excluded. These data confirm the high incidence of secondary nectar thievery by honey bees in southeastern blueberry plantations (Delaplane 1995) as well as the inability of honey bees to act as primary nectar thieves. Nectar thievery by honey bees is dependent on the primary thieving activity of *Xylocopa* spp. during which the corollae receive the perforations that are subsequently preferred by honey bees.

Under ambient orchard conditions, temporal changes in the incidence of honey bee robbing behavior were explained by Mitscherlich asymptotic growth models (Fig. 1) in which rates of illegitimate honey bee flower visitation increase from initial lows to fixation at $\geq 95\%$. For 2001, the model predicted that the incidence of honey bee robbing behavior would achieve 95% by Julian day 97 (x_p , of a range of observed days Julian 92–113). The same value for 2002 was Julian day 90 (range of observed days Julian 87–107). We propose two explanations for the temporal increase in robbing behavior by honey bees: increasing availability of flowers perforated by *X. virginica* and/or learned preferential transition by honey bees from legitimate to illegitimate foraging. The first explanation is only weakly supported by the data. Once *X. virginica* were strongly active in the orchard (>22 March 2001 and >1 April 2002), the average incidence of flowers perforated in the open plots generally increased over the three consecutive weekly sampling periods beginning 1–2 April (30.6 ± 4.5 , 30.2 ± 4.6 , and $42.9 \pm 7.1\%$ for weeks 1–3, respectively), but not significantly ($F = 2.8$; $df = 2, 1$; $P \geq 0.4$). Instead, the

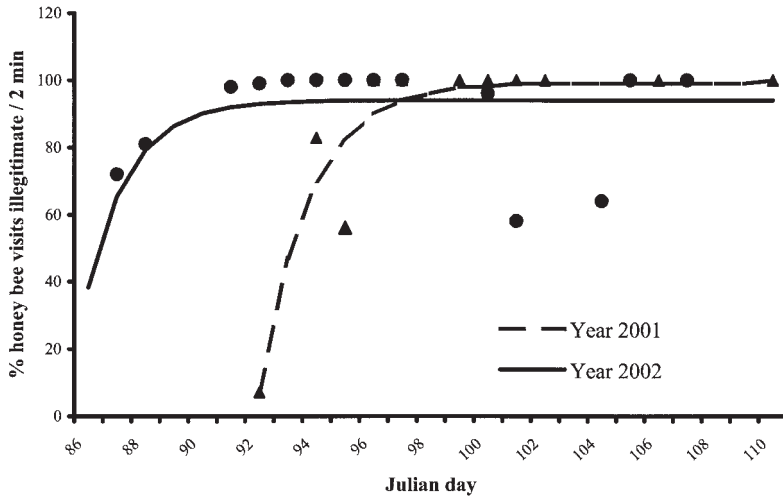


Fig. 1. Relationship between Julian day (x) and percentage of honey bee flower visits illegitimate/2 min (y) in open plots of ‘Climax’ rabbiteye blueberry. Observed values (2001, \blacktriangle ; 2002, \bullet) are percentage of honey bee visit illegitimate, and the lines connect predicted values from Mitscherlich asymptotic growth models (Ware et al. 1982): $y_{2001} = 100 (1 - 0.05e^{-0.56(x - 97.2)})$, $r^2 = 0.88$; $y_{2002} = 100 (1 - 0.05e^{-0.67(x - 89.7)})$, $r^2 = 0.86$.

average range of 30.2–42.9% open flowers perforated was achieved early then remained static. Therefore, honey bees do not seem to be responding to temporal variation in the availability of perforated flowers. However, when the relationship between proportion of honey bee visits illegitimate and proportion of flowers perforated was examined independently of time, almost all the variation ($r^2 = 0.99$) was explained by a Mitscherlich asymptotic growth model (Fig. 2), which predicts that illegitimate foraging by honey bees increases from initial lows to fixation at $\geq 95\%$ once the incidence of perforated flowers achieves 50% (x_p). Collectively, these analyses suggest that the incidence of perforated flowers in an orchard rapidly

achieves static levels but that honey bees learn quickly to preferentially visit flowers illegitimately, reaching near fixation in the expression of this behavior. Indeed, we note a type of flower rejection behavior in honey bees by which the forager inspects the proximal base of corollae and rejects those without perforations. In one sampling interval in 2001, these rejections constituted 21.9 ± 10.3 ($n = 3$) of honey bee flower visits in the AX plots. Honey bees are known to express similar learned transitions in flower handling behavior in other crop species, most notably alfalfa, *Medicago sativa* L., in which the bees learn to avoid tripping the sexual column, thus avoiding a blow to the head (Free 1993).

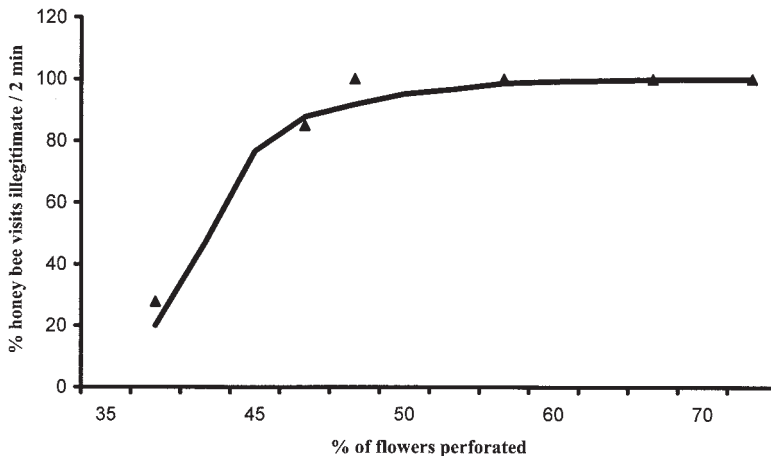


Fig. 2. Relationship between percentage of flowers perforated (x) and percentage of honey bee flower visits illegitimate/2 min (y) in open plots of ‘Climax’ rabbiteye blueberry. Observed values (\blacktriangle) are percentage of honey bee visits illegitimate and the line connects predicted values from the Mitscherlich asymptotic growth model (Ware et al. 1982): $y = 100 (1 - 0.05e^{-0.19(x - 50.0)})$, $r^2 = 0.99$.

Table 2. Fruit characteristics (number of mature seeds per berry and weight of berry) of 'Climax' rabbiteye blueberry as affected by honey bees and carpenter bees in tents (≈ 2 by 2 m)

Treatment Year	Mature seeds/berry		Berry weight (g)	
	2001	2002	2001	2002
Open	14.6 \pm 1.4b (25)	24.4 \pm 1.0a (86)	1.4 \pm 0.1a (25)	1.5 \pm 0.04b (88)
A	18.6 \pm 1.3a (38)	17.0 \pm 1.0b (63)	0.8 \pm 0.05b (38)	1.6 \pm 0.05a (65)
AX	10.3 \pm 0.7c (37)	10.6 \pm 0.7c (64)	1.07 \pm 0.06b (37)	1.2 \pm 0.04c (65)
X	3.1 \pm 0.6d (26)	0.7 \pm 0.3d (35)	0.9 \pm 0.07b (28)	0.9 \pm 0.06d (34)
0	0.5 \pm 0.2d (17)	0.08 \pm 0.06d (38)	0.8 \pm 0.09b (17)	1.0 \pm 0.05d (39)

Five treatments were organized as follows: 3,200 honey bees and two carpenter bees combined in one tent (*Apis/Xylocopa*, AX), two carpenter bees (*Xylocopa*, X), honey bees (*Apis*, A), no bees (0), and open plot (open). Treatment interacted with year for seed number and berry weight; hence, data are herein reported by year (2001 and 2002). Values are mean \pm standard error, with *n* in parentheses. Means within a column followed by the same letter are not significantly different at the $\alpha = 0.05$ level.

Fruit Set. Fruit set was affected by treatment ($F = 13.6$; $df = 4, 5$; $P = 0.0068$), but there were no year effects or interactions of treatment with year ($F = 4.0$; $df = 1$ or $4, 5$; $P \leq 0.0822$). Fruit set was significantly higher in the A, AX, and open plots than X or 0 plots (Table 1). These results support earlier work showing that *A. mellifera* is an effective pollinator of rabbiteye blueberry variety 'Climax' (Sampson and Cane 2000; Dedej and Delaplane 2003). The similarity in fruit set between A and AX plots is noteworthy considering that the incidence of illegitimate flower visits by honey bees approached 40% in the AX plots (Table 1). Moreover, commercially acceptable yields are produced in orchards in which the incidence of illegitimate honey bee visitation meets or exceeds 95% (Fig. 1). Even though bees were excluded from the 0 plots, an average background of 25.1% fruit set (selfing) is implicated with *V. ashei* 'Climax' in this orchard (Table 1). Although *V. ashei* is considered self-sterile, there is a degree of variation in the expression of this character (Meador and Darrow 1944).

Five derivative hypotheses follow from these observations: 1) fruit set is not compromised by rates of illegitimate honey bee visitation approaching 40%; 2) repeat flower visits by colonial *A. mellifera* effect a degree of compensation for illegitimate visits, given that illegitimate flower visitors are generally inefficient pollinators (Inouye 1980) and that *V. ashei* 'Climax' responds positively to repeat legitimate honey bee visits (Dedej and Delaplane 2003); 3) a disproportionately high amount of honey bee-induced fruit set occurs before the bees learn to seek robbery perforations (naïve honey bees are comparatively efficient pollinators; Delaplane and Mayer 2000); 4) honey bees effect acceptable pollination even at extremely low rates of legitimate flower visitation (unsupported by Dedej and Delaplane 2003); and/or 5) there is a high degree of compensatory pollination by other legitimate flower visitors, namely, *Bombus* spp. Latreille and *Habropoda laboriosa* (F.) (Cane and Payne 1990, Stout et al. 2000).

Seed Number. For this variable there were no year effects ($F = 1.5$; $df = 1, 5$; $P = 0.2785$), but there was a significant interaction between treatment and year ($F = 6.0$; $df = 4, 5$; $P = 0.0378$) so seed number was analyzed by year. There were significant treatment effects in 2001 ($F = 46.5$; $df = 4, 138$; $P < 0.0001$) and

2002 ($F = 123.8$; $df = 4, 281$; $P < 0.0001$). Mean separations are shown in Table 2. The interaction is explained by the inversion of rankings between the open and A plots in the 2 yr.

The number of seeds is a good indicator of the effectiveness of the pollinator as well as a measure of female fertility if compatible pollen is abundant (Ritzinger and Lyrene 1998). Fruits had similarly low number of seeds in plots with no bees or only *X. virginica*, whereas the highest seed numbers were achieved in open or A plots (Table 2). The most interesting observation is the comparison of seed numbers between the A and AX plots. In both years, there was a reduction of seeds when *A. mellifera* was tented with *X. virginica* (AX plots). This, coupled with the fact that illegitimate flower visitation by honey bees was nearly 40% in the AX plots (Table 1), indicates that *X. virginica*-induced nectar robbery by *A. mellifera* compromises the pollination efficacy of *A. mellifera* in *V. ashei* as measured in seed set. If seed set continues to drop at increasing rates of secondary nectar thievery, this may have negative effects on fruit set under ambient conditions where rates of illegitimate honey bee visitation meet or exceed 95% (Fig. 1). Some of our observations support this idea. In 3 yr of field studies (including the present work), we have noted evidence that our orchard is naturally pollinated at levels below its physiological capacity. Fruit set tends to be lower in open plots than in tented plots in which honey bee densities are optimized (Table 1, current study; Table 1, Dedej and Delaplane 2003). It is likely that *X. virginica*-induced robbing behavior by *A. mellifera* contributes to this ambient pollination deficit. This effect may be exaggerated in commercial plantations of *V. ashei* where imported honey bees are the most numerous bee visitor (Delaplane 1995) and their diversion more damaging. It may be possible to improve the efficacy of honey bees by increasing hive densities and/or moving hives into the orchard after bloom has commenced, practices believed, respectively, to increase the overall number of honey bee foragers and the number of naïve foragers (Delaplane and Mayer 2000). Alternatively, increasing the density of non-*Apis* pollinators is an appropriate response, but these bees are comparatively difficult to manage (Delaplane and Mayer 2000). Another approach is to

develop practices that minimize the impact of primary nectar thievery by *Xylocopa* spp.

In general the effects of nectar robbers are a result of complex interactions between the taxa of plants as well as those of legitimate and illegitimate flower visitors (Malooof and Inouye 2000). Indeed, the effects of robbers can range from benign to beneficial, as shown by Malooof (2001) who not only failed to detect a negative effect of nectar thievery on fruit set and seed set in *C. caseana* A. Gray but also suggested that the activity of robbers induces longer interfloral flight by legitimate visitors thus increasing rates of outcrossing.

Finally, we note that fruit set remains high in AX plots in spite of a significant decrease in seed set by *A. mellifera* in the presence of *X. virginica* (Tables 1 and 2). To the five derivative hypotheses we offer above, we now add a tentative sixth: 6) there is at least a partial physiological independence of fruit set from seed set in *V. ashei*. Support for this hypothesis is found in our earlier independent work (Dedej and Delaplane 2003), but seed set and fruit set vary positively in the data of Gupton and Spiers (1994) for rabbiteye and MacKenzie (1997) for highbush cultivars.

Berry Weight. This variable expressed a significant year effect ($F = 12.8$; $df = 1, 5$; $P = 0.016$) as well as an interaction between treatment and year ($F = 5.4$; $df = 4, 5$; $P = 0.0466$), so it was analyzed by year. There were significant treatment effects in 2001 ($F = 8.0$; $df = 4, 140$; $P < 0.0001$) and 2002 ($F = 32.9$; $df = 4, 286$; $P < 0.0001$). Mean separations are shown in Table 2. Average berry weight (grams) was higher in 2002 (1.3 ± 0.02 , mean \pm SE, $n = 291$) than in 2001 (1.0 ± 0.04 , $n = 145$). The interaction of treatment with year (Table 2) is best explained by the comparatively low sample sizes of 2001 combined with an inversion of rankings between the 2 yr for the open and A plots. However, for 2002 there is evidence that berry weight was higher in open, A, and AX plots over that in 0 or X plots. It is possible that berry weight in *V. ashei* does not respond consistently to variation in pollinator efficiency; Dedej and Delaplane (2003) failed to detect differences in berry weight across a continuum of honey bee densities. However, it is generally expected in *Vaccinium* spp. that berry weight will vary positively with seed number (Filmer and Marucci 1963, Dorr and Martin 1966, Brewer and Dobson 1969, Moore et al. 1972), but this trend is not universal, as demonstrated by MacKenzie (1997) in highbush blueberry.

Sucrose Content. None of the independent variables significantly affected the percentage of sucrose content of fruit juice ($F \leq 5.0$; $df = 1$ or $4, 5$; $P \geq 0.0767$). Our mean value range of 13.7–16.0% is generally higher than that of ≈ 10 –13.5% reported by Austin and Bondari (1993) for 'Climax'. There was a trend in the data toward higher sucrose content in those plots experiencing the poorest pollination (Table 1), a tendency noted before (Dedej and Delaplane 2003). Cross-pollination is known to increase total sugar content in highbush blueberry (Kobashi et al. 2002).

Speed of Ripening. Speed of fruit ripening was unaffected by any of the independent variables ($F \leq 3.9$; $df = 1$ or $4, 5$; $P \geq 0.1038$). Excepting the AX plot, there was a trend in the data for faster ripening in those plots experiencing superior pollination (Table 1). Cross-pollination with compatible pollen is known to improve speed of ripening in highbush (MacKenzie 1997) and rabbiteye blueberries (Gupton and Spiers 1994).

In conclusion, our data confirm a high incidence of primary nectar thievery by *X. virginica* in southeastern *V. ashei* plantations, the inability of honey bees to engage in primary thievery, and a high incidence of secondary thievery by honey bees, and implicate a learned preference by honey bees for corollae formerly perforated by *X. virginica*. Under tent conditions, the continuous presence of two carpenter bees per two mature bushes results in nearly 40% incidence of *A. mellifera* robbery. This level of secondary nectar thievery does not reduce fruit set but does reduce the number of seeds per berry, an important physiological indicator of pollinator efficacy. There seems to be a partial independence of fruit set from seed set in *V. ashei* (fruit set is optimal [Table 1] in plots in which seeds/berry is suboptimal [Table 2]). But if seed set is further reduced under ambient conditions where the incidence of secondary thievery meets or exceeds 95% (Fig. 1), then it is possible that secondary thievery eventually exacts a cost on fruit set. This scenario may explain the suboptimal fruit set we have observed under ambient orchard conditions.

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