

Association Between Density of Foraging Bees and Fruit Set in Commercial Fields of Rabbiteye Blueberries (*Ericales: Ericaceae*) in Louisiana and Mississippi

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Abstract

Field-scale data on the relationship between pollinator activity and fruit set are scarce for rabbiteye blueberries (*Vaccinium virgatum* Aiton). We measured the densities of *Apis mellifera* L. (Hymenoptera: Apidae), *Habropoda laboriosa* F. (Hymenoptera: Apidae), *Bombus* Latreille (Hymenoptera: Apidae) spp., and *Xylocopa virginica* L. (Hymenoptera: Apidae) in 7–21 commercial fields during each of 3 yr in Louisiana and Mississippi. Foraging bees were counted on 10 ‘Tifblue’ bushes per field on 2 d during bloom, and the density of bees per flower was calculated based on the number of flowers open during the counts. Fruit set was measured 30 d after bloom. The impact of foraging activity on fruit set was inconsistent when densities of either all foragers or foragers of individual taxa were considered. Strong associations were observed only in 2001, with fruit set increased by *H. laboriosa* and *Bombus* and with a weaker contribution by *A. mellifera*. Floral robbery by *X. virginica* had no measurable negative effects. Populations of *H. laboriosa* were more consistent than those of other bees across sites. Managed colonies of *A. mellifera* were added at two densities (12.5 or 2.5 colonies per hectare) in seven fields each in 2001. These supplemental bees did not result in greater forager densities or fruit set in stocked fields. The observations show the challenge of field-scale pollination tests but provide an initial framework for rabbiteye blueberry growers to assess the availability of foraging bees early in bloom to help decide whether to add supplemental *A. mellifera* to try to enhance pollination if populations of non-*Apis* bees are low.

Key words: *Vaccinium virgatum*, pollination, *Apis mellifera*, *Habropoda laboriosa*, *Xylocopa virginica*

Cultivated rabbiteye blueberries (*Vaccinium virgatum* syn. *ashei* Aiton) and southern highbush blueberries (*Vaccinium corymbosum* L. × *Vaccinium darrowii* Camp. [Ericales: Ericaceae] hybrids) are grown on 10,000 hectares in the southeastern United States and had a farm gate value of \$200 million in 2012 (NASS 2012). Cultivars of *V. virgatum* are largely self-incompatible and require cross pollination for acceptable fruit set (Meador and Darrow 1944). Several insects are responsible for vectoring pollen, cross pollinating flowers, and setting fruit. Among them, bees, principally native bees such as the southeastern blueberry bee (*Habropoda laboriosa* F.) and bumble bees (*Bombus* Latreille spp.), are effective pollinators according to stigmatic pollen deposition per floral visit (Cane and Payne 1990, Payne et al. 1991, Cane 1997). The capability of carpenter bees (principally *Xylocopa virginica* L.) to cross pollinate *V. virgatum* bushes is enigmatic. Bees cut slits through the base of the corolla and apparently avoid the anthers and stigmas during these

floral ‘robbing’ visits, but studies regarding the effect of this behavior on *V. virgatum* fruit set have yielded mixed information, i.e., a positive effect on pollen deposition, a neutral effect on fruit set (Sampson et al. 2004), and a negative effect on seed set (Dedej and Delaplane 2004). At a landscape scale, populations of all native bees tend to vary spatially and temporally, making it challenging to rely on these unmanaged resident species for pollination in commercial cropping systems (Cane and Payne 1993).

Managed honey bees (*Apis mellifera* L.) sometimes are used as supplemental pollinators for rabbiteye blueberries. The effectiveness of honey bees as pollinators, however, is somewhat in dispute. They generally are less efficient pollinators than other species (Cane and Payne 1990, Sampson and Cane 2000). Inefficiency may arise because honey bees 1) have relatively short tongues that may not reach the base of the tubular corollas, 2) are unable to sonicate ericaceous blossoms and release large quantities of pollen, 3) may visit

higher-reward flowers rather than blueberries, and 4) often forage by using slits cut by carpenter bees in the base of the corolla rather than by accessing resources through the normal opening at the apex of the flower (Delaplane 1995). Pollination efficacy appears to vary by cultivar, e.g., honey bees are less efficient pollinators than other bee species on 'Tifblue' (Cane and Payne 1990), and are more effective pollinators of 'Climax' than of 'Tifblue' (Sampson and Cane 2000). Fruit set on rabbiteye plants in cages was found to be better with honey bees than in cages without bees by Whatley and Lockett (1979) but not by Ambrose and Mainland (1979).

Because blueberry orchards may be managed to have supplemental honey bee colonies during bloom for pollination, it is important to know whether fruit production depends on honey bee density. In a study using rabbiteye plants and honey bees in pollinator-exclusion cages, Dedej and Delaplane (2003) found that 'Climax' set more fruit when caged with greater densities of bees. It is not known, however, how results from cage studies translate to field settings. We explored this issue by describing the relationship between densities of foraging bees and fruit set in commercial fields of rabbiteye blueberries in Louisiana and Mississippi during three seasons. The observations occurred on 'Tifblue', the most widely grown cultivar. Our objectives were to determine the relationships of densities of the four most common bee taxa with fruit set; spatial and temporal variation of bee taxa; and effects on fruit set of honey bee density under conditions of natural and supplemented populations.

Materials and Methods

Observations were made on 'Tifblue' plants in commercial blueberry fields in Louisiana and Mississippi in spring of 2001 (21 fields), 2002 (11 fields), and 2003 (10 fields). Fields ranged in size from 0.4 to 30.4 ha (2001, 3.3 ± 5.3 [sd] ha; 2002, 7.7 ± 10.8 ha; 2003, 3.9 ± 9.2 ha) and consisted of handpicked, 'U-pick' and mechanically harvested operations. Only four of the same fields were observed in all 3 yr.

In 2001, seven fields each were stocked with commercially managed colonies of honey bees at rates of 2.5 or 12.5 colonies per

hectare (one or five colonies per acre) for the duration of the bloom period; also, there were seven unstocked fields. Colonies had about six deep Langstroth frames covered with bees and were housed in hives having one deep and one medium box. We did not supplement any orchards with honey bee colonies in 2002 or 2003.

We selected 10 representative bushes in each field for monitoring forager abundances and fruit set. Densities of foraging *A. mellifera*, *Bombus* spp., *H. laboriosa*, and *X. virginica* (the only bee taxa we saw) were measured on 2 d each year (once during early bloom and once during mid bloom, between mid March and mid April) when conditions were favorable for foraging, i.e., $\geq 21^\circ\text{C}$, sunny, and with wind ≤ 16 km/h. Instantaneous counts of foraging bees were made on each bush two to four times between 10.00 and 14.00 h by two observers walking along the rows. Bee counts were averaged within each day and then over both days. We recorded the percentage of *X. virginica* foragers that were robbing flowers by cutting slits through corollas. The number of open flowers on each bush was estimated on each day by sampling four spaces within the flowering canopy and extrapolating to the entire plant based on the height and diameter of the canopy. For each sample space, we counted the number of open flowers within an imaginary wedge bounded by a 25×25 -cm square on the vertical outer surface of the flowering canopy and connected to 25 cm of the vertical central axis of the bush (Fig. 1). We also recorded the percentage of open flowers in these spaces that had corollas slit, presumably by foraging *X. virginica*. The densities of foraging bees of each species at each site were calculated from the average number of bees per 1,000 open flowers on each of the 10 bushes. The densities of foragers of all four taxa were summed to create a count of 'all bees'.

Fruit set was measured by selecting four or five shoots with a total of ~ 100 flower buds on each of the 10 bushes during early bloom, and counting fruit ~ 30 d after flowering. Counting fruit ~ 30 d after bloom was thought to be late enough to account for the drop of nonpollinated or poorly pollinated fruit, but early enough to avoid fruit loss unrelated to pollination before ripening (e.g., by herbivory). *Vaccinium virgatum* has been shown to hold fruit well

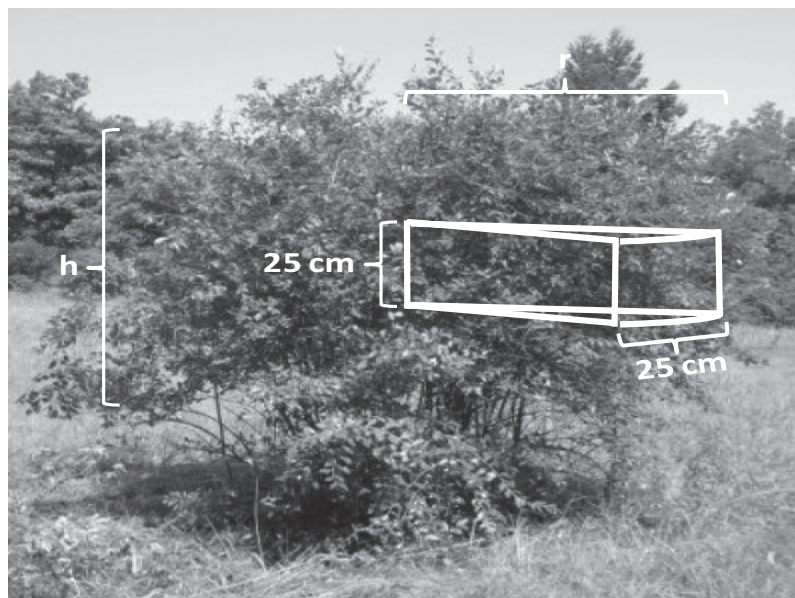


Fig. 1. Procedure for sampling the number of flowers in each plant of *V. virgatum*. The number of flowers counted in four wedge-shaped spaces (the boundary of one wedge is indicated by the heavy white lines; see text) were used to estimate the total number of flowers in the volume of the cylindrical canopy. The canopy volume (indicated by black dashed lines) is $\pi r^2 h$, where r = radius and h = height.

after unrestricted visitation by pollinators (Sampson et al. 2013). We tested this in 2001 by measuring fruit set both 30 d after bloom and again when fruits began changing color during ripening. Early fruit set was correlated with later fruit set (Pearson's correlation, $r = 0.849$, $n = 21$, $P < 0.001$), so we used only early fruit set thereafter in 2002 and 2003. Frost damage to flowers and young fruit prevented the use of data from two fields in northern Louisiana in 2002 and 2003, and one field in Mississippi in 2003. We were unable to make a second count of foragers in two fields in 2003.

Analysis of variance (ANOVA; Proc Mixed; SAS Institute 2010) was used to test for effects of years and (for 2001 data) for stocking density. ANOVA proceeded after bee counts and fruit set data were determined to be normally distributed (Shapiro–Wilk in Proc Univariate) and with homogenous variances (Levene's Test in Proc Anova). Effects of honey bee density on fruit set were estimated by regression analysis (Proc Reg) with the option selection=maxr. General relationships between variables were assessed with Pearson's correlation analysis.

Results and Discussion

An initial analysis of observations from all fields in all years ($n = 37$) showed an adequate average green fruit set for 'Tifblue' rabbiteye blueberry of $73 \pm 2\%$ (SE). Forager densities (calculated as bees per 1,000 flowers) overall were 2.37 ± 0.42 for *A. mellifera*, 0.52 ± 0.17 for *H. laboriosa*, 0.17 ± 0.04 for *Bombus*, and 0.10 ± 0.03 for *X. virginica*. *Apis mellifera* was observed in all 37 fields we used across 3 yr, *H. laboriosa* in 30 fields, *Bombus* in 21 fields, and *X. virginiana* in 15 fields. Overall, the density of neither any single bee taxon nor the combined density of foragers from all taxa was strongly related to fruit set, although the density of *H. laboriosa* across all years

approached significance ($P = 0.070$) (Table 1). This weak relationship was probably due to no clear association between fruit set and the densities of foragers of any bee species or the combination of all species in 2002 and 2003 (Table 1). However, in the 2001 season, fruit set was strongly related to the density of foragers of all bee taxa combined (Table 1). The relationship appeared asymptotic (Fig. 2), and regression analysis confirmed that fruit set improved as foraging density increased up to 3.3 bees per 1,000 flowers ($F = 9.05$; $df = 1,14$; $P = 0.009$; $R^2 = 0.39$). The effect of the densities of bees of individual taxa followed similar patterns. The density of *A. mellifera* on fruit set trended toward significance ($P = 0.060$), and regression analysis confirmed that fruit set improved as the density of *A. mellifera* increased up to 3.0 foragers per 1,000 flowers ($F = 5.25$, $df = 1,16$; $P = 0.036$; $R^2 = 0.25$). Densities of *A. mellifera* greater than this did not increase fruit set. *Habropoda laboriosa* at all densities improved fruit set and had the greatest effect at densities up to 0.3 bees per 1,000 flowers ($F = 8.46$, $df = 1,10$; $P = 0.016$; $R^2 = 0.46$). *Bombus* at all densities improved fruit set and had the greatest effect at densities up to 0.06 bees per 1,000 flowers ($F = 16.18$, $df = 1,12$; $P = 0.002$; $R^2 = 0.57$). Densities of *X. virginica* foragers had less clear of an effect on fruit set ($P = 0.078$).

Bee densities at our study sites varied greatly between years. Densities of *A. mellifera*, *Bombus*, and *X. virginica* were significantly greater in 2003 than in the first 2 yr (Table 2). Among the 37 fields analyzed, we used only four fields in all 3 yr; the between-year variation in forager densities also occurred in those four fields (data not shown). Despite this between-year variation in forager densities, the within-year order of the densities of the taxa was consistently *A. mellifera* > *H. laboriosa* > *Bombus* > *X. virginica*. Notably, only the density of *H. laboriosa* did not differ between years. This finding of annual spatial reliability agrees with the findings of Cane

Table 1. Regression coefficients and associated probabilities relating mean forager density of four bee taxa to fruit set of 'Tifblue' rabbiteye blueberries

| | All years | | 2001 | | 2002 | | 2003 | |
|----------------------------|-----------|-------|-------|-------|-------|-------|-------|-------|
| | r^2 | P | r^2 | P | r^2 | P | r^2 | P |
| All bees | 0.005 | 0.898 | 0.303 | 0.010 | 0.006 | 0.838 | 0.004 | 0.888 |
| <i>Apis mellifera</i> | 0.006 | 0.658 | 0.174 | 0.060 | 0.008 | 0.825 | 0.091 | 0.510 |
| <i>Habropoda laboriosa</i> | 0.091 | 0.070 | 0.247 | 0.022 | 0.000 | 0.966 | 0.302 | 0.202 |
| <i>Bombus</i> spp. | 0.013 | 0.510 | 0.230 | 0.028 | 0.056 | 0.542 | 0.013 | 0.806 |
| <i>Xylocopa virginica</i> | 0.002 | 0.800 | 0.154 | 0.078 | 0.146 | 0.310 | 0.001 | 0.943 |

Foragers were observed in 21 fields in 2001, 9 in 2002, and 7 in 2003.

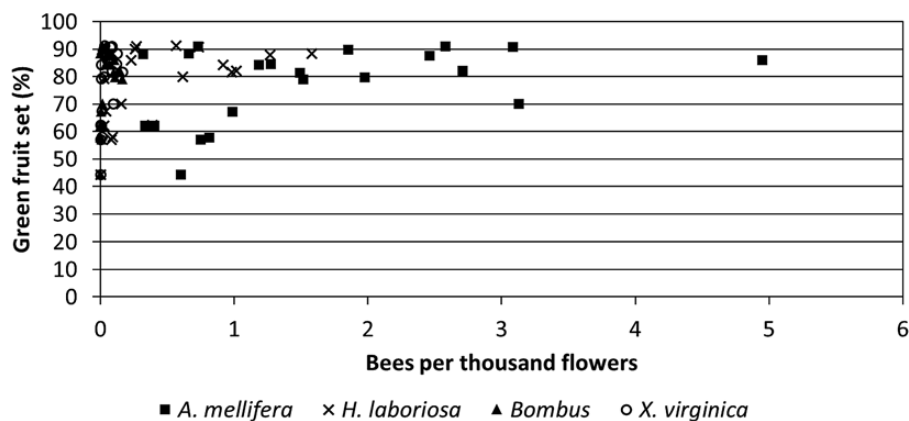


Fig. 2. Relationship between the mean density of foraging bees of four taxa and green fruit set in 21 fields in 2001.

Table 2. Mean \pm SE of forager density (bees per 1,000 flowers) and fruit set in commercial orchards of 'Tifblue' rabbiteye blueberry

| | 2001 | 2002 | 2003 |
|----------------------------|------------------|------------------|------------------|
| All bees | 2.15 \pm 0.31b | 1.42 \pm 0.34b | 8.45 \pm 1.70a |
| <i>Apis mellifera</i> | 1.61 \pm 0.26b | 1.04 \pm 0.29b | 6.40 \pm 1.21a |
| <i>Habropoda laboriosa</i> | 0.45 \pm 0.10a | 0.24 \pm 0.10a | 1.11 \pm 0.83a |
| <i>Bombus</i> spp. | 0.05 \pm 0.01b | 0.12 \pm 0.04b | 0.59 \pm 0.15a |
| <i>Xylocopa virginica</i> | 0.05 \pm 0.01b | 0.02 \pm 0.01b | 0.35 \pm 0.15a |
| Fruit set | 77 \pm 3a | 67 \pm 2b | 67 \pm 5b |

Foragers were observed in 21 fields in 2001, 9 in 2002, and 7 in 2003. Fruit set is based on green fruit existing ~30 d after the end of bloom. Values within rows that do not share a letter differ at $P \leq 0.05$.

and Payne (1993) and may be due to gregarious females establishing well-concealed nests in sandy woodland sites along the periphery of blueberry fields (Cane 1994). Rabbiteye blueberry growers should be able to determine whether their growing area has a resident population of *H. laboriosa* and can use this knowledge, together with knowledge of historical fruit production, to inform decisions about adding supplemental pollinators. Female *H. laboriosa* are efficacious blueberry pollinators because of their strong trophic specialization on blueberry pollen and capacity to sonicate ('buzz-pollinate') *Vaccinium* flowers (Cane and Payne 1988). *Habropoda laboriosa* had a positive effect on fruit set at densities of only 10% of those of *A. mellifera*. This is consistent with results from more narrowly defined studies of pollination efficiency (Cane and Payne 1990) in which visits from non-*Apis* bees than from *A. mellifera* provided better fruit set. Our field results thus support the current Extension Service recommendations that encourage growers to recognize the value of non-*Apis* bees for pollination (Himelrick et al. 1995, Williamson et al. 2004).

Although *X. virginica* were the least abundant of the pollinators, their floral robbery may affect blueberry cross pollination and resulting fruit set (Sampson et al. 2004). The frequency of robbing we observed by foraging *X. virginica* varied from 0 to 100% among fields (average 47% for early counts and 58% for later counts). The percentage of slit flowers followed a similar pattern (range 0–81% [average 27%] for early counts and range 1–72% [average 31%] for later counts). Robbing of 'Tifblue' flowers by *X. virginica* overall tended to be correlated positively with fruit set ($r = 0.435$, $P = 0.055$, $n = 20$), but slitting was not ($r = 0.171$, $P = 0.436$, $n = 23$). This finding indicates a possible threshold effect whereby a flower that has been robbed eventually receives sufficient pollen to set fruit from *A. mellifera* foraging through the slit in the corolla (Sampson et al. 2004).

After recognizing that smaller fields tended to have both greater fruit set ($r = -0.314$, $P = 0.059$, $n = 37$) and perhaps a greater density of all foraging bees ($r = -0.290$, $P = 0.081$, $n = 37$), we performed a third analysis on only our largest fields (≥ 2.0 ha [≥ 5 acres]) where bee densities were significantly less (Table 3). In these 14 large fields, forager density affected fruit set both for all bees ($F = 8.18$, $df = 1,12$; $P = 0.014$; $R^2 = 0.405$) and for individual bee taxa across all years (Fig. 3). The density of *A. mellifera* had the strongest effect on fruit set ($F = 9.70$, $df = 1,12$; $P = 0.009$; $R^2 = 0.447$). Densities of *H. laboriosa* ($F = 5.72$, $df = 1,12$; $P = 0.034$; $R^2 = 0.323$) and *X. virginica* ($F = 5.57$, $df = 1,12$; $P = 0.036$; $R^2 = 0.317$) had strong effects, while the density of *Bombus* had a weaker effect ($F = 4.16$, $df = 1,12$; $P = 0.064$; $R^2 = 0.257$). This result confirms the value of honey bees as blueberry pollinators in fields where supplementation normally would be warranted. The limited number of large fields precluded more detailed analysis of density effects, e.g., by year and by stocking rate of managed honey bee colonies

Table 3. Mean \pm SE of forager density (bees per 1,000 flowers) and fruit set in larger (≥ 2.1 ha; $n = 14$) and smaller (< 2.1 ha; $n = 23$) orchards of 'Tifblue' rabbiteye blueberry across 3 yr

| | Large | Small |
|----------------------------|-----------------|-----------------|
| All bees | 2.39 \pm 1.00 | 3.64 \pm 0.66 |
| <i>Apis mellifera</i> | 1.63 \pm 0.52 | 2.83 \pm 0.59 |
| <i>Habropoda laboriosa</i> | 0.63 \pm 0.43 | 0.46 \pm 0.09 |
| <i>Bombus</i> spp. | 0.11 \pm 0.07 | 0.21 \pm 0.05 |
| <i>Xylocopa virginica</i> | 0.02 \pm 0.01 | 0.15 \pm 0.05 |
| Fruit set | 67 \pm 3 | 76 \pm 3 |

Fruit set is based on green fruit existing ~30 d after the end of bloom. Values within each row differ at $P \leq 0.05$.

The landscape surrounding blueberry fields may also affect the density of foraging *A. mellifera*. Although there was some indication that *A. mellifera* improved fruit set in 2001, neither fruit set ($F = 0.24$; $df = 2,18$, $P = 0.787$) nor density of *A. mellifera* foragers ($F = 0.16$; $df = 2,18$, $P = 0.852$) were affected by the stocking rate of honey bee colonies we added to some fields that year. *Apis mellifera* comprised about 75% of bees in fields of each treatment group (Table 4). Fields having no or few supplemental colonies were well represented among those that had a high density of *A. mellifera* foragers and had high fruit set. The lack of differences in *A. mellifera* densities and fruit set in fields stocked at different rates with managed colonies was surprising. These findings may indicate that *A. mellifera* sometimes foraged on more rewarding host plants away from the blueberry fields (Payne et al. 1991). A lack of correlation between honey bee stocking rate and forager density on blueberry bushes also may have resulted simply from unknown sources of feral or managed honey bees near our fields, or from imprecise measuring of foraging activity and fruit set in field settings despite multiple sampling of foragers and eliminating observable problems of frost damage that affected fruit set.

Our observations of pollinator densities may provide a basis for growers to assess the adequacy of foraging activity in rabbiteye blueberry fields during early bloom and then attempt to adjust pollination activity. Tagged shoots on our focal plants had $33 \pm 2\%$ of flowers open at early bloom counts (67% of flowers remained as buds). These early counts generally followed the averages of the two counts in most cases, and so seemed to accurately reflect the forager density in the field. The data suggest that rabbiteye blueberry growers should strive to have an average of at least three bees total per 1,000 flowers to optimize pollination if the primary bees seen are honey bees. Our census data also indicate that ~0.3–0.4 native bees (*H. laboriosa* and *Bombus*) per 1,000 flowers would be an adequate density to provide cross pollination in rabbiteye blueberry fields.

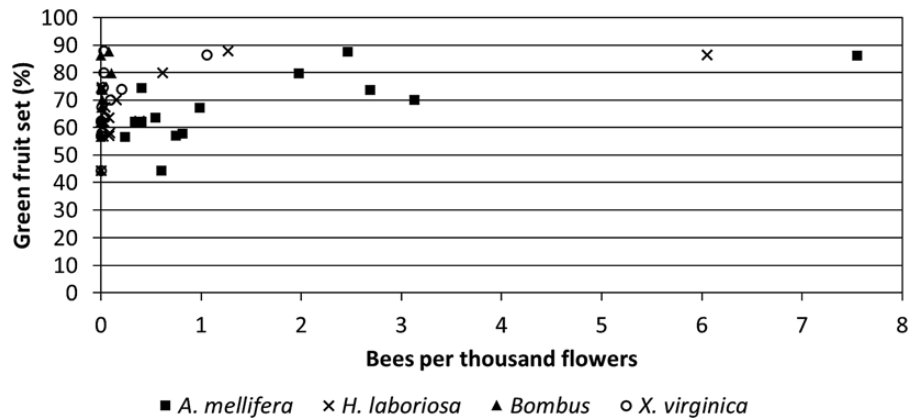


Fig. 3. Relationship between the mean density of foraging bees of four taxa and green fruit set during three years in the 14 fields that were ≥ 2.0 ha (≥ 5 acres) in area.

Table 4. Densities of foragers and green fruit set (mean \pm SE) in fields stocked at different rates with honey bee colonies in 2001

| | 0 colony/ha | 2.5 colony/ha | 12.5 colonies/ha |
|----------------------------|-----------------|-----------------|------------------|
| All bees | 2.36 \pm 0.53 | 2.30 \pm 0.70 | 1.79 \pm 0.37 |
| <i>Apis mellifera</i> | 1.72 \pm 0.40 | 1.71 \pm 0.61 | 1.39 \pm 0.35 |
| <i>Habropoda laboriosa</i> | 0.56 \pm 0.14 | 0.47 \pm 0.18 | 0.31 \pm 0.21 |
| <i>Bombus</i> spp. | 0.04 \pm 0.01 | 0.05 \pm 0.02 | 0.06 \pm 0.02 |
| <i>Xylocopa virginica</i> | 0.04 \pm 0.01 | 0.07 \pm 0.02 | 0.03 \pm 0.02 |
| Fruit set (%) | 80.1 \pm 5.4 | 74.8 \pm 6.4 | 77.4 \pm 4.1 |
| Hectares | 3.1 \pm 1.0 | 5.5 \pm 3.4 | 1.3 \pm 0.4 |

There were seven fields at each stocking rate. There were no differences in densities of *A. mellifera* between fields stocked at different rates.

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