

ORIGINAL CONTRIBUTION

Bee visit rates vary with floral morphology among highbush blueberry cultivars (*Vaccinium corymbosum* L.)

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Abstract

As the human population has increased, so too has the demand for biotically pollinated crops. Bees (*Apoidea*) are essential for pollen transfer and fruit production in many crops, and their visit patterns can be influenced by floral morphology. Here, we considered the role of floral morphology on visit rates and behaviour of managed honey bees (*Apis mellifera*) and wild bumble bees (genus *Bombus*), for four highbush blueberry cultivars (*Vaccinium corymbosum* L.). We measured five floral traits for each cultivar, finding significant variation among cultivars. Corolla throat diameter may be the main morphological determinant of visit rates of honey bees, which is significantly higher on the wider flowers of cv. 'Duke' than on 'Bluecrop' or 'Draper'. Honey bees also visited cv. 'Duke' legitimately but were frequent nectar robbers on the long, narrow flowers of cv. 'Bluecrop'. Bumble bees were infrequent (and absent on cv. 'Draper') but all observed visits were legitimate. Crop yield was highest for the cultivar with the highest combined (honey bee + bumble bee) visit rate, suggesting that aspects of floral morphology that affect pollinator visit patterns should be considered in crop breeding initiatives.

Introduction

The vast majority of angiosperms rely on animal pollinators to reproduce (Ollerton et al. 2011). Although the degree to which pollinators are essential for plant reproduction varies among species, over one-third of the world's agricultural crops require animal-mediated pollination, primarily by bees, for production (Klein et al. 2007). Understanding the pollination process in crop plants is especially important given recent documented declines in some wild and managed pollinator populations (Biesmeijer et al. 2006; Kosior et al. 2007; National Research Council 2007; Cameron et al. 2011). Here, we make the case for considering the importance of flower morphology for pollination in highbush blueberry, *Vaccinium corymbosum* L.

Flower morphology is known to affect pollinator visit rate and the suite of pollinators that visit flowers (e.g. Bell 1985; Conner 1997; Wilson et al. 2004; Kudo and Harder 2005; Martén-Rodríguez et al.

2009). Important cues for pollinators include colour (e.g. Schemske and Bradshaw 1999), scent (e.g. Raguso and Willis 2002) and especially the quantity and quality of nectar and pollen rewards (e.g. Aronne et al. 2012), but visit rates are also associated with flower size (e.g. Elle and Carney 2003) or morphology-related limits to reward accessibility (e.g. Herrera 1989; Stang et al. 2009). Limits on access to rewards may encourage nectar-robbing behaviour, where bees access nectar rewards illegitimately through holes in the corolla, often without pollen removal or delivery (Irwin et al. 2010). Although the importance of floral morphology for plant-pollinator interactions has been well studied in wild plant species, it is rarely the focus of study for crop plants, despite having the potential to impact yields. In most cases, cultivated varieties are the result of selective breeding for yield under particular environmental conditions (Evenson and Gollin 2003), but such breeding may additionally give rise to variation in morphology. Flower number and the size

of the standard petal affected outcrossing rate in beans (*Vicia faba*, Suso et al. 2008), and stigma exertion affected both pollinator behaviour and outcrossing rates in tomato (*Lycopersicon pimpinellifolium*, Rick et al. 1978). In citrus (genus *Citrus*), cultivars differed in nectar quality, which affected visit rates and yield (Wolf et al. 1999). In blueberry (*Vaccinium* spp.), floral shape variation among species and among lowbush blueberry (*Vaccinium angustifolium*) cultivars determined whether honey bees (*Apis mellifera*) could reach nectaries and affect pollination (Free 1993). Cultivars within commercially grown highbush blueberry (*Vaccinium corymbosum*) may also vary in flower morphology. Our goal was to assess this variation, and its impact on pollinator visit patterns and crop yield.

The specialized morphology of *Vaccinium* flowers (fig. 1) has great potential to impact pollinator efficacy. Blueberry flowers have poricidal dehiscent anthers, requiring sonication (buzz-pollination) to release pollen, and are therefore less capable of

passive self-pollination than other floral morphologies (Buchmann 1983), although facilitated selfing can occur. Bumble bees (*Bombus* spp.) are capable of sonicating flowers to release pollen (Goulson 2010), but honey bees are not, and primarily forage for nectar on blueberry (Dogterom and Winston 1999). When pollen-foraging honey bees work poricidal anthers, they tend to do so inefficiently by tapping the anthers with their legs, removing little pollen (Cane et al. 1993). Taken together, this means that bumble bees are more efficient blueberry pollinators, delivering more pollen to stigmas on a per-flower basis than managed honey bees (Javorek et al. 2002). In addition, bumble bees generally have longer tongues than honey bees (Goulson 2010), with the result that blueberry cultivars with longer or narrower corollas may limit access by honey bees to nectar rewards (Free 1993), increasing handling time, decreasing the rate of resource acquisition, and consequently encouraging nectar robbing. Thus, according to optimal foraging theory (Pyke 1984), variation in morphology among cultivars is expected to influence the visit rate of managed honey bees to different cultivars of commercial highbush blueberry, as well as their ability to pollinate this crop effectively.

In this study, we asked whether cultivars of highbush blueberry varied in flower morphology, whether floral morphology influenced pollinator visit rates, and whether any differences in pollinator visit patterns translated into differences in fruit set among cultivars. We predicted that cultivars with larger corolla throat diameters or shorter corolla tubes would be visited more often by managed honey bees and wild bumble bees, due to greater ease of access to nectar rewards. Greater access to floral rewards should result in greater visit rates and therefore higher fruit set than other flower morphologies.

Methods

Study sites

In 2010, British Columbia accounted for 95% of Canada's total marketable volume of highbush blueberries (*Vaccinium corymbosum*; Government of Canada 2012). Highbush blueberry is grown agriculturally throughout the Metro Vancouver and Fraser Valley Regional Districts in British Columbia, Canada. Individual farms range from 4–100 ha and are embedded in a matrix of blueberry and cranberry farms with a smaller component of the surrounding area comprised of other agriculture, semi-natural areas and suburban neighbourhoods. Individual shrubs can be quite large

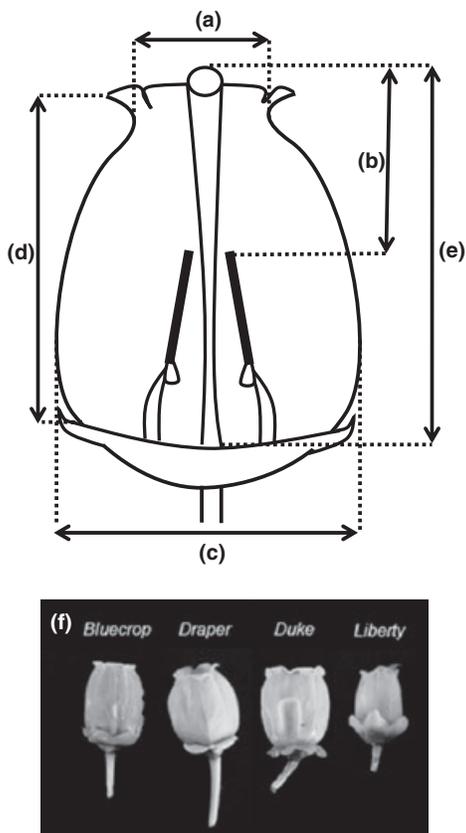


Fig. 1 Measurements taken for blueberry flowers include: (a) throat diameter; (b) distance between the anthers and the stigma; (c) corolla width; (d) corolla length; and (e) style length. Typical flower morphology for the four cultivars studied is shown in (f).

(0.75–2 m tall; Supporting Information Figure S1) and bloom for approximately 3–4 weeks in spring (starting in May in our region).

We analysed four cultivars commonly grown in our region: Bluecrop, Draper, Duke and Liberty (fig. 1). Bluecrop and Duke cultivars were paired at three different sites located in the municipalities of Abbotsford, Pitt Meadows, and Delta. Draper and Liberty cultivars were paired at two sites both located in Abbotsford. No farms grew all four cultivars of interest, although cv. Duke is frequently cultivated in our region and is grown within 1 km of all sites. Commercial honey bee colonies were present at all sites during crop bloom.

Flower morphology

We expected floral morphology to differ among cultivars largely because cultivars are vegetatively propagated genetic clones. However, we subsampled within fields in case environmental conditions such as edge effects have an influence on floral morphology. Ten plants were selected along each of two or three 100 m transects located at increasing distances from the most natural edge of the field (0 m and 100 m in Draper and Liberty; 0 m, 50 m, and 100 m in Bluecrop and Duke). Transects were split into 10 m intervals, and plants were chosen at random distances within each interval. Flowers open from the bottom to the top of the inflorescence, so to eliminate flower age as a determinate of variation in morphology among cultivars, we collected the second youngest flower (second open flower from the tip) from one inflorescence per plant for morphometric measurements. Flowers were preserved in 95% ethanol and frozen until measurements could be completed in the laboratory.

Blueberry flowers are urn-shaped, and we took measurements to capture variation of this shape among cultivars (fig. 1). Using digital callipers, we measured total length of the flower from the base of the floral tube to the opening of the corolla, the corolla throat (opening) diameter, and the width of the corolla at the widest point. We then used a scalpel to make a slit in the corolla to allow measurement of the length of the style and the distance between the anthers and the stigma while those organs were still *in situ*. Anther-stigma distance should affect the ability of cultivars to self-pollinate, with smaller distances potentially allowing for more selfing. Although variation in nectar quantity or quality also may affect pollinator behaviour in blueberry, we were unable to collect sufficient quantities of nectar to include this variable in our study.

Pollinator observations

Pollinators were observed between 10 May and 10 June 2012, on days in which weather patterns were conducive to pollinator activity. These were non-rainy days with full or part sun, temperatures above 13°C and low wind. We observed insect visitors on each of 10 plants per transect for one minute each. Observations were performed along the same transects where morphology was assessed, and plants were again chosen in the same stratified random fashion described earlier. We completed three replicate observation events for each Bluecrop and Duke site and two replicates for each Liberty and Draper site. Multiple sites were assessed within a given date (between the approximate hours of 10 AM and 4 PM), in random order, such that each site was observed both morning and afternoon in case there is a bias in the timing of pollinator activity. A total of 15 observation dates were needed to complete this number of replicate sampling events. We recorded the number of individual insects that visited flowers, their species if possible, the number of flowers visited per insect and behaviour for honey bees. We noted whether honey bees inserted their proboscis or entire head into the flower (interpreted as a legitimate visit), or whether they robbed nectar by inserting the proboscis between the corolla and inferior ovary, thereby avoiding contact with the anthers (Supporting Information Figure S2). All bumble bee visits observed were legitimate, so bumble bee behaviour could not be analysed. Observations were summed across transects within date for analyses due to the high number of zero values.

Fruit set

We marked branches with 10 to 20 flowers on all plants for which flowers used for morphological measurements were sampled. We noted the number of flowers on the selected branch and allowed pollination to occur naturally. Once the branches produced fruit, we counted the number of fruit and calculated the relative fruit set (fruits/flower) for each plant within each transect. Because transects did not differ in fruit set in initial analyses, and to allow better comparison with the pollinator visit data, relative fruit set was averaged by transect within each field, and each transect was treated as a replicate for analysis.

Statistical analysis

We used SAS 9.2 software (SAS Institute 2008) and R statistical software (R Core Team 2012) for analyses.

We natural log-transformed the corolla throat diameter, corolla width, and bumble bee and honey bee visit rates prior to analysis to eliminate heteroscedasticity. For honey bee visit data, we added 1 to values prior to transformation as we had a few (7) zero values in the data set. Bumble bee data had a large number of zeros (40 of 70 observations) and so needed to be analysed differently than honey bee data, see below.

To determine whether cultivars differed in the suite of measured floral traits, we performed a mixed-model multivariate analysis of variance (MANOVA, in SAS) with site as a random variable, followed by univariate ANOVAs to evaluate which of the five measured traits contributed to cultivar differences. We initially included distance in this analysis but removed it from final models as it was never significant. To test whether honey bee visits differed by cultivar, we carried out a mixed-model ANOVA in SAS with site and replicate as random factors and used a Tukey–Kramer test to determine differences between visit rates among cultivars. Because so many bumble bee visit values were zero, we analysed bumble bee visit rates

using a two-step process. We first determined whether there was a difference between cultivars in the likelihood of being visited at all using a chi-square test of presence/absence data for bumble bee visits, in R. We then analysed only those instances in which bumble bee visits were greater than zero using the same mixed-model ANOVA (in SAS), as for honeybees, to determine whether cultivar affected log-transformed bumble bee visit rates.

We used a mixed-model ANOVA in SAS with site as a random factor to evaluate differences in proportion fruit set among cultivars, using logit-transformed data (Warton and Hui 2011) for analysis. Finally, we used a G-test in SAS to determine whether the three categories of honey bee visit behaviour (inserting proboscis, inserting head, robbing) differed among cultivars.

Results

Morphology

Floral morphology varied among highbush blueberry cultivars (figs 1 and 2). The MANOVA indicated overall

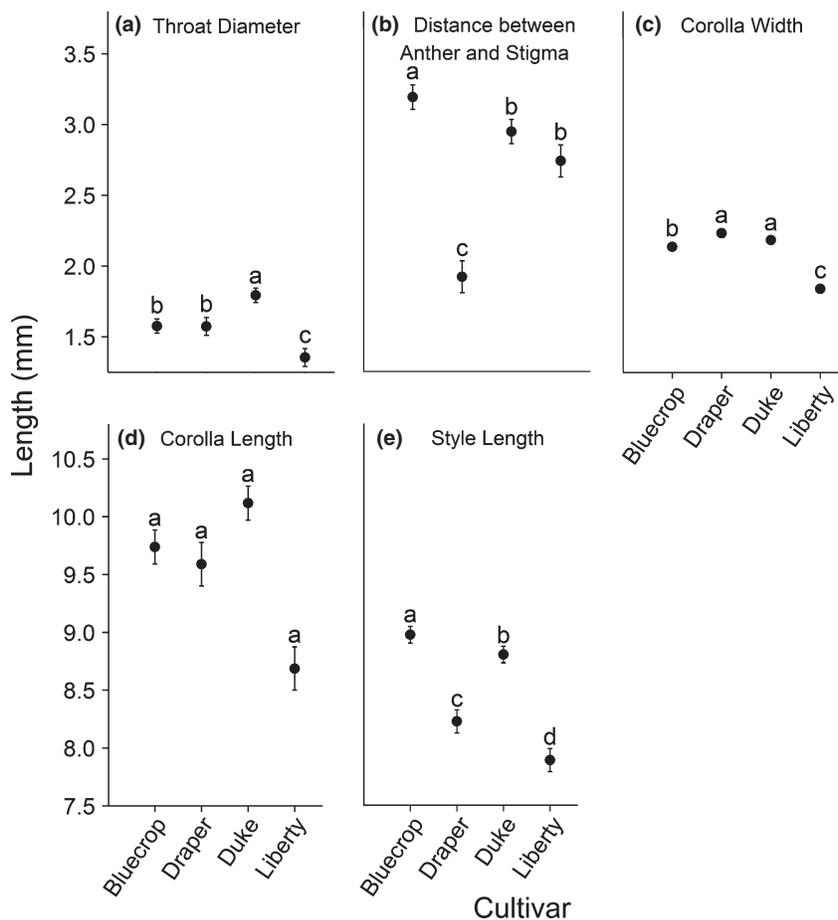


Fig. 2 Comparisons of floral measurements [(a) throat diameter; (b) distance between the anthers and the stigma; (c) corolla width; (d) corolla length; and (e) style length] for four blueberry cultivars: Bluecrop, Draper, Duke and Liberty. Whiskers indicate one standard deviation from the mean. Within morphological variables, means with the same letter are not significantly different. Throat diameter and corolla width were log-transformed for analysis but untransformed means are presented here.

differences among cultivars (Wilk's lambda, $F_{15,5.92} = 18.61$, $P = 0.0009$). Univariate ANOVAS followed by post hoc tests demonstrated that Duke flowers had a larger corolla throat diameter ($F_{3,245} = 8.92$, $P = 0.012$) than all other cultivars, wider corollas ($F_{3,245} = 20.08$, $P = 0.002$) than Bluecrop and Liberty and tended to have longer corollas ($F_{3,245} = 3.68$, $P = 0.08$) than the other cultivars (fig. 2). Duke and Bluecrop had longer styles than Liberty and Draper flowers ($F_{3,245} = 10.86$, $P = 0.008$). Draper flowers had the smallest anther-stigma distance ($F_{3,245} = 19.09$, $P = 0.002$) and so may have a greater potential for self-pollination. Liberty flowers had narrower corollas, a narrower corolla throat diameter, and a shorter style than other cultivars.

Pollinator observations

Honey bee visit rates differed among cultivars ($F_{3,61} = 5.87$, $P = 0.0014$). Duke was visited significantly more often than Draper and Bluecrop, but did not differ from Liberty (fig. 3). There was a significant

effect of cultivar on bumble bee presence, with Duke, Bluecrop and Liberty more likely to be visited than Draper ($\chi^2 = 10.83$, d.f. = 3, $P = 0.013$). There was no further effect of cultivar on bumble bee visit rate once zero values were removed ($F_{2,23} = 0.63$, $P = 0.54$). When considering total visit rate (honey bees and bumble bees combined), Duke had higher visit rate (20.1 on average per transect) than Bluecrop (10.1 visits) and Draper (8.5 visits), but did not differ significantly from Liberty (14 visits; $F_{3,61} = 6.02$, $P = 0.0012$).

Honey bee behaviour

Visiting behaviour of honey bees differed significantly among cultivars (fig. 4; $G = 67.52$, $P < 0.0001$). Of the honey bees that visited Duke, 78% inserted their entire head into the flower, increasing the likelihood of pollen deposition on their face. Honey bees were more likely to rob Bluecrop flowers than the other cultivars, with a 42.7% robbing rate. Draper and Liberty had similar proportions of legitimate visits as

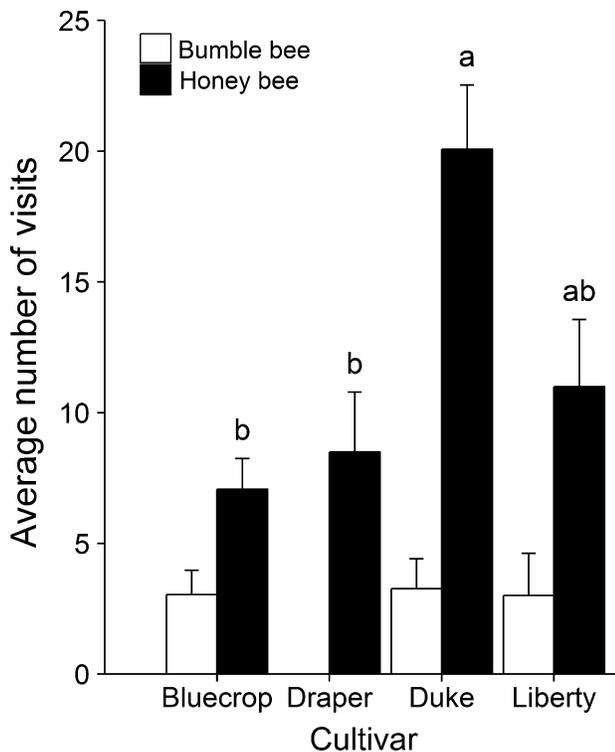


Fig. 3 Comparison of total bumble bee and honey bee visits for blueberry cultivars Bluecrop, Draper, Duke and Liberty. Whiskers indicate one standard error from the mean. Within honey bees, means with the same letter are not significantly different. For bumble bees, presence was higher in Bluecrop, Duke and Liberty than in Draper (zero visits observed), but once zero values were removed from analysis, there was no difference among cultivars (see Results).

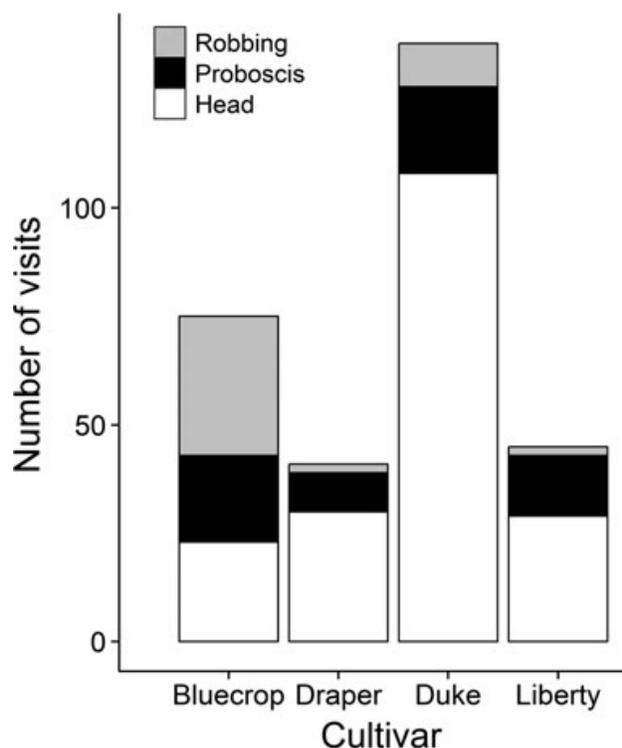


Fig. 4 Number of times different honey bee behaviours were exhibited when visiting highbush blueberry, which differs significantly among cultivars. 'Robbing' indicates that the proboscis was inserted between the corolla and inferior ovary to reach nectar, 'proboscis' indicates only the proboscis was inserted into the corolla tube and 'head' indicates complete insertion of head into corolla.

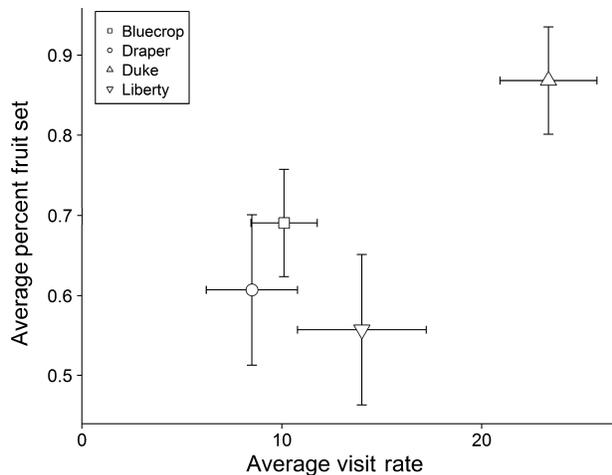


Fig. 5 The average relative fruit set by the average visit rate of bumble bees and honey bees combined for blueberry cultivars Bluecrop, Draper, Duke and Liberty. Whiskers denote one standard error from the mean. Note that average fruit set is not logit-transformed for presentation purposes although analysis was conducted on transformed data.

Duke, with 73.2% and 64.4% of visiting honey bees inserting their entire head into the flowers.

Fruit set

We found that relative fruit set was significantly different among cultivars (fig. 5). Duke had the highest relative fruit set of the four cultivars, but Bluecrop, Draper and Liberty did not differ from each other ($F_{3,19} = 4.19$, $P = 0.02$). Fruit set appears related to total visit rate to cultivars (fig. 5), because Duke differs greatly from the other cultivars for fruit set and from Bluecrop and Draper for visit rate.

Discussion

Floral morphology differed significantly between highbush blueberry cultivars Bluecrop, Draper, Duke and Liberty, and the cultivar with larger floral openings (Duke) was visited more than two of the others (Bluecrop and Draper) and had the highest fruit set. Although many studies of wild plant species suggest that floral morphology plays a large role in plant–pollinator interactions (e.g. Bell 1985; Herrera 1989; Conner 1997; Wilson et al. 2004; Martín-Rodríguez et al. 2009; Stang et al. 2009), crop species have not been well studied in this context, despite the importance of plant–pollinator interactions for yield (Klein et al. 2007).

We predicted that floral morphologies with larger throat diameters and shorter corollas would have greater visitation rates than narrower or longer corol-

las. Duke flowers do have the largest throat diameter (1.79 ± 0.017 mm, fig. 3), but also have marginally longer corollas (10.1 ± 0.060 mm) than other cultivars. We suggest that the wider throat diameter may improve honey bee access to floral rewards. The effective tongue length of honeybees ranges between 6.4 and 7 mm (Free 1993); although head width is on average wider than throat diameter (3.96 ± 0.02 mm; D. Courcelles, unpublished data), we observed that honeybees could force their entire head into the throats of Duke flowers due to the flexible nature of the corolla tissue (fig. 4). This apparently increased honey bee effective tongue length enough to allow them to reach nectar rewards. In contrast, although Bluecrop flowers were shorter (9.73 ± 0.054 mm), their narrower throat diameter (1.58 ± 0.013 mm) apparently restricted access by honey bees to nectar, perhaps explaining the higher frequency of nectar robbing in this cultivar. Draper and Liberty had shorter corollas than Duke (Draper: 9.59 ± 0.101 mm; Liberty: 8.69 ± 0.101 mm), with narrow corolla throat diameters (Draper: 1.57 ± 0.021 mm; Liberty: 1.35 ± 0.021 mm). In Draper, this combination of floral traits may explain significantly lower visit rates compared with Duke. In Liberty, although the throat diameter was small, corollas may have been short enough (approximately 1 mm shorter than all others) that nectar could be accessed and honeybee handling time was not strongly affected. Ability of honey bees to access nectar in Liberty could explain why there was less reduction in visit rate than the throat diameter would predict (not significantly different from Duke).

Variation in flower morphology may aid in explaining Marucci's (1966) findings that honey bees exhibit preferences for specific cultivars when foraging on blueberry. Morphological changes that impact handling time and access to floral rewards are expected to affect foraging choices (Pyke 1984; e.g. Aronne et al. 2012). Similarly, insect morphology affects visit patterns; Cane and Payne (1993) explained visit rate differences among bee species on rabbiteye blueberry (*V. ashei*) as at least partially due to differences in bee species tongue lengths, which affect their ability to efficiently access rewards. Although honey bees were one of the most common visitors to rabbiteye blueberry, they frequently robbed flowers and were thought to be ineffective pollinators as a result (Cane and Payne 1993). Similarly, we find that honey bees are likely relatively ineffective pollinators of highbush blueberry cv. Bluecrop due to their tendency to nectar rob.

All of our farms had similar honeybee stocking rates, and so differences in honey bee availability

should not be the cause of differences in average visit rates among cultivars. However, at all of our sites, Duke was well within foraging distance (<1 km from focal fields) of honey bees, which can forage up to several kilometres from the location of the colony (Visscher and Seeley 1982; Beekman and Ratnieks 2000). If our differences in visit rate are truly due to a preference of honey bees for the commonly grown cv. Duke floral morphology, then honey bees stocked in Bluecrop, Draper and Liberty fields may be preferentially foraging on Duke flowers outside our focal fields. Although we could not collect adequate nectar for analysis, if Duke additionally has greater nectar quantity or quality than other cultivars studied, we would expect foraging preferences for Duke to be especially strong.

For many crops, production increases with biotic pollination (Klein et al. 2007). This increase is true even for crops such as okra and cucumber (*Abelmoschus esculentus* and *Cucumis sativus*; Free 1993) that are capable of passive self-pollination. We therefore predicted that blueberry floral morphologies that had higher pollinator visit rates would exhibit higher relative fruit sets than other morphologies. Duke had significantly higher relative fruit set than Bluecrop, Draper and Liberty and was visited more often than Bluecrop and Draper. Although honey bees are less effective pollinators than bumble bees on a per-flower basis for plant species with dehiscent poricidal anthers (Javorek et al. 2002), when few bumble bees are present in blueberry fields (as in our study), higher visit rates by honey bees may increase relative fruit set substantially.

Some highbush blueberry cultivars have high yield even when hand pollinated with self-pollen (MacKenzie 1997; Dogterom et al. 2000). Although reduced anther-stigma separation is expected to increase self-pollen transfer (Lloyd and Schoen 1992), the shorter anther-stigma distance in Draper flowers did not translate into greater relative fruit set. Fruit set in Draper was not significantly different from either Bluecrop or Liberty, suggesting that bees are required for pollination and yield in Draper. Ratti et al. (2008) suggest that high bumble bee abundance, and not honey bee abundance, is important for blueberry yield in our study region. However, the proportion of visits by bumble bees in our agricultural landscapes was low; 73 of 623 observed visits (11.7%), compared with 45.6% of bees collected in gardens of the Metro Vancouver area (Tommasi et al. 2004) and 22.5% of bees collected in natural areas on Vancouver Island, B.C. (Neame et al. 2013). Bumble bees may be uncommon in agricultural landscapes if

surrounding areas provide inadequate forage outside of the short bloom period of the crop (Kennedy et al. 2013). Bumble bee populations near our sites may be inadequate to affect fruit set for cultivars that would benefit most from bumble bee visits—those that are not preferred by honey bees (Bluecrop and Draper in our study). We suggest that efforts to increase bumble bee populations will likely improve fruit set and thus overall production in these cultivars.

There is evidence of pollinator declines in North America (Committee on the Status of Pollinators in North America 2007; Cameron et al. 2011), although this trend is poorly understood for all pollinator species (Cane and Tepedino 2001). If North American wild pollinators are in decline, as Cameron et al. (2011) have found with four bumble bee species, agriculturalists will be required to increase their reliance on managed honey bees to pollinate crops. An increase in demand for crops which rely on biotic pollination is already occurring, but the current supply of honey bee colonies will be unable to meet growing demand (Aizen and Harder 2009). Recent research suggests that wild bees contribute more to crop pollination worldwide than honey bees do (Garibaldi et al. 2013), but that wild bee abundance is linked to the combination of on-farm practices and surrounding landscape (Kennedy et al. 2013). With the increased difficulty in acquiring honey bee colonies and declines in wild bee populations, crop production of biotically pollinated species may also be at risk, but our results suggest the degree of risk will vary among cultivars within a crop species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. View of a field of highbush blueberry (*Vaccinium corymbosum* cv. Duke) in full bloom. Plants are approximately 1 m tall. Cultivars Liberty and Draper tend to be similar in size in our region (occasionally shorter, 0.5 m tall), and cultivar Bluecrop is larger, approximately 1.5 m on average. (L. Button photo)

Figure S2 (a) Legitimate visit by *Bombus melanopygus* to cv. Duke. (b) Nectar robbing by *Apis mellifera* to cv. Bluecrop. (E. Elle photos)