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RESEARCH ARTICLE

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Optimal foraging by honey bees (*Apis mellifera*) reduces cross-cultivar visitation in highbush blueberry (*Vaccinium corymbosum*): implications for pollination efficiency in monocultures

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Inter-cultivar pollination is essential for high-quality blueberry production, as it increases both fruit set and fruit size. In commercial orchards, this is often achieved by alternating blueberry cultivars across rows, based on the assumption that honey bees move pollen between cultivars by switching rows. However, honey bee movement patterns in orchards remain understudied, and it is unclear whether this design effectively supports inter-cultivar pollination. To address this knowledge gap in a South African context, we determined the frequency of honey bee foraging movements across versus along blueberry rows. While observing a focal foraging honey bee, we recorded the number of flowers visited on a blueberry bush, whether the bee transitioned between plants, and whether these transitions occurred along or across a row. Our observations revealed that honey bees predominantly foraged along rows (over 90% of transitions), rarely switching across rows. Consequently, alternating cultivars by row is likely to limit inter-cultivar pollination in South African blueberry orchards, potentially reducing yield. We recommend interplanting compatible cultivars within rows to enhance pollen transfer and fruit production. Given that honey bees are used globally as the primary managed pollinator, similar movement patterns may occur in other regions, suggesting that modifying planting designs could increase yields of blueberries and other bee-pollinated crops with minimal additional cost. However, these findings are based on observations from a single commercial orchard and should be replicated across multiple farms and environmental conditions to determine the generality of these patterns.

INTRODUCTION

Clonal crops have become increasingly important in agriculture due to their uniformity, which facilitates management and consistent crop production. Currently, clonal crops span at least 34 plant families (McKey et al. 2010). However, a significant challenge with clonal cultivars is their genetic uniformity, which often leads to inbreeding depression and necessitates outcrossing for successful sexual reproduction (Zohary 1984). In clonal crop systems, outcrossing depends on effective pollen transfer between different cultivars, prompting growers to plant multiple cultivars in adjacent blocks or alternating rows to encourage pollinator-mediated cross-pollination (Schneider et al. 2005; Yildiz et al. 2014; MacInnis & Forrest 2020). Honey bees (*Apis mellifera*) are the most widely used commercial pollinators and are expected to facilitate pollen movement between cultivars. Yet, the spatial arrangement of crops may not align with honey bee foraging behaviour, potentially limiting the efficiency of cross-cultivar pollen transfer.

In typical row-planted systems, intra-row plant spacing is usually smaller than inter-row spacing, influenced by operational needs such as machinery movement and harvesting. According to optimal foraging theory, pollinators minimize energy expenditure by visiting flowers in close proximity, often favouring movements along rows rather than between rows (Pyke 1984). Such behaviour can result in repeated visitation of nearby plants or cultivars within a row, reflecting row-restricted foraging patterns that are conceptually related to trapline foraging and may reduce cross-cultivar pollen flow, with downstream consequences for fruit set and abortion (Karron et al. 2009; Ohashi & Thomson 2009). Evidence from other crop systems supports this: honey bees foraging on dwarf apples predominantly visited single trees or adjacent trees within the same row (Free & Spencer-Booth 1964), and similar row-restricted foraging patterns were observed in almonds (Brittain et al. 2013).

This study focuses on honey bee foraging behaviour in highbush blueberry (*Vaccinium corymbosum*) monocultures, where inter-cultivar pollination enhances fruit yield by an average of 42% compared to intra-cultivar pollination (Martin et al. 2025). Successful blueberry production thus depends on pollinators moving pollen across cultivars (Mackenzie & Eickwort 1996; Dogterom et al. 2000; Fulton et al. 2015). While native blueberry pollinators include large-bodied bees like bumble bees, which are highly effective (Mackenzie & Eickwort 1996; Javorek et al. 2002; Tuell et al. 2009; Campbell et al. 2017, 2018), honey bees remain the primary commercial pollinators globally due to their availability and manageability, even where bumble bees coexist (Aras et al. 1996; Birstein et al. 1997; Fulton et al. 2015; Gibbs et al. 2016; Hoffman et al. 2018). In regions outside the native range of bumble bees, such as southern Africa and Australasia, honey bees are often the sole managed pollinators supporting entire blueberry industries. Previous work by Martin et al. (2021) showed that honey bees significantly increased berry mass by 53% relative to no pollination, but yield improvements between 23% and 66% suggest that honey bee pollination may still be suboptimal for some cultivars (Martin et al. 2022).

Here, we present a case study examining honey bee foraging patterns in blueberry orchards, focusing on the frequency of movements within versus between rows. Given the row planting design, where intra-row distances are shorter than inter-row gaps (Pyke 1984, 2019), we hypothesised that honey bees would predominantly forage along rows, exhibiting row-restricted foraging behaviour that limits cross-row cultivar visitation and, consequently, cross-pollination potential.

MATERIALS AND METHODS

Study site and observations

To assess natural foraging behaviour in a commercial context, honey bee movement patterns were observed across several days between August and October 2021 in a one-hectare solid-block planting of the southern highbush blueberry cultivar Ventura (*Vaccinium corymbosum* L. hybrid) on a commercial blueberry farm near Paarl, Western Cape, South Africa (33°48′30.7″ S, 18°54′09.8″ E). The block comprised approximately 7 500 plants and was stocked with 15 managed honey bee (*Apis mellifera*) hives, corresponding to hive densities typically used in commercial blueberry production systems (Isaacs & Kirk 2010; Gibbs et al. 2016; Hoffman et al. 2018). Honey bee hives were positioned both along the perimeter of the shade-netted block and within the shade-net tunnels, reflecting typical hive placement practices in commercial blueberry orchards under netting. The orchard was surrounded predominantly by agricultural land (mainly vineyards), with the Simonsberg Nature Reserve located approximately 3 km from the study site. All plants were grown under shade-net structures. Observations were conducted under favourable weather conditions, characterised by sunny, calm conditions with little to no wind and daytime temperatures ranging between approximately 18 and 25 °C. Observations were conducted during daylight hours when honey bee activity was high, primarily between mid-morning and early afternoon, and coincided with peak bloom of the blueberry crop, when the majority of flowers were open and receptive.

The blueberry plants were arranged in rows spaced 2.6 m apart to allow for mechanical and human access. This spacing meant that branches did not overlap across rows. Within each row, plants were spaced 0.75 m apart, and branches overlapped between adjacent plants. This layout reflects typical planting arrangements used in commercial blueberry orchards in southern Africa (Coen Groenewald, personal communication). Honey bee colonies were stocked at a density of fifteen hives per hectare, which falls within the commercial range observed across other blueberry farms (ranging from four to 39.5 hives per hectare) as reported in previous studies (Isaacs & Kirk 2010; Gibbs et al. 2016; Hoffman et al. 2018).

Foraging behaviour was recorded by selecting a single honey bee that was actively visiting blueberry flowers. A visit was considered successful when the bee inserted its head into the corolla of a flower. For each foraging sequence, we recorded the number of flowers visited per plant, the transitions between plants, and whether those transitions occurred along the same row or across rows. Observations were only included in the dataset if the same bee could be followed for at least two successive plant visits. Observations were stopped if the bee returned to the hive, was lost from sight, or if its identity could no longer be confirmed with certainty. During observations, the observer remained approximately 1.5 m from focal flowers, close enough to reliably track individual bees while avoiding any interference with foraging behaviour. In total, 90 honey bee foraging trips were successfully recorded over a period of seven days, resulting in approximately 24 hours of observational data.

Statistical Analyses

We used several statistical approaches to evaluate whether honey bee foraging movements occurred more frequently along rows than across rows. First, a chi-square test was performed to determine whether transitions between plants occurred at equal frequencies in the two directions. Under a random foraging scenario, equal proportions of along-row and across-row movements would be expected.

Second, we performed a logistic regression analysis to determine the likelihood of a foraging movement occurring across a row. In this model, each movement was classified as either an along-row (scored as 0) or an across-row transition (scored as 1). The analysis was based on observations of 90 individual bees whose movements were recorded in this way.

To evaluate whether the number of plants visited varied according to movement direction, we fitted a linear mixed-effects model with movement direction (along-row or across-row) as a fixed effect. Honey bee identity was included as a random effect, allowing both slope and intercept to vary without covariance. The model met the assumptions of normality and homoscedasticity, as assessed through Q–Q plots of the residuals.

Post hoc comparisons between movement directions were carried out using Tukey's linear contrasts. We also calculated Nakagawa's R^2 values (Nakagawa & Schielzeth 2013) to assess model fit. Marginal R^2 values represent the proportion of variance explained by fixed effects alone, while conditional R^2 values reflect the variance explained by both fixed and random effects. When these two values are similar, it indicates that most of the variance is explained by the fixed effect; larger differences suggest greater influence from individual-level variation captured by the random effect.

Finally, we used a Mann–Whitney–Wilcoxon test to compare the frequency of movements within individual plants versus movements between different plants. All statistical analyses were performed using R version 3.3.2.

RESULTS

Approximately 70% of observed honey bees foraged exclusively along rows of blueberry plants, while no individuals foraged exclusively across rows (Figure 1A). The remaining 30% of bees displayed mixed movement patterns, making transitions both along and across rows. However, even in these cases, movements were heavily biased with the vast majority of transitions occurring along rows rather than across them (Figure 1B).

When honey bees move between plants, they move along rows more frequently (92% of the time) than expected by chance and across rows less frequently (8%) than expected by chance ($\chi^2 = 253.34$, df = 1, $p < 0.001$, Figure 1B). Similarly, the logistic regression showed that as a honey bee moves from plant to plant the likelihood of it switching across a row is only 6.24%, while the likelihood that it switches along a row is 93.76% ($z = -5.52$, $p < 0.001$).

The conditional variance for the honey bee movement model was $R^2_c = 0.55$, with the marginal variance being $R^2_m = 0.49$. On average, honey bees made an order of magnitude more ($z = -13.96$, $p < 0.001$) along-row transitions (mean ± SE = 3.67 ± 0.25 plants, Figure 2) between blueberry plants than across row transitions between blueberry plants (0.32 ± 0.06 plants, Figure 2). Similarly, honey bees transitioned between plants far less frequently (21%) when compared to within plants (79%) ($v = 54$, $p < 0.001$).

DISCUSSION

Under the conditions of this study, honey bees did not forage randomly within a commercial blueberry orchard. Specifically, honey bees foraged along rows and very rarely moved across

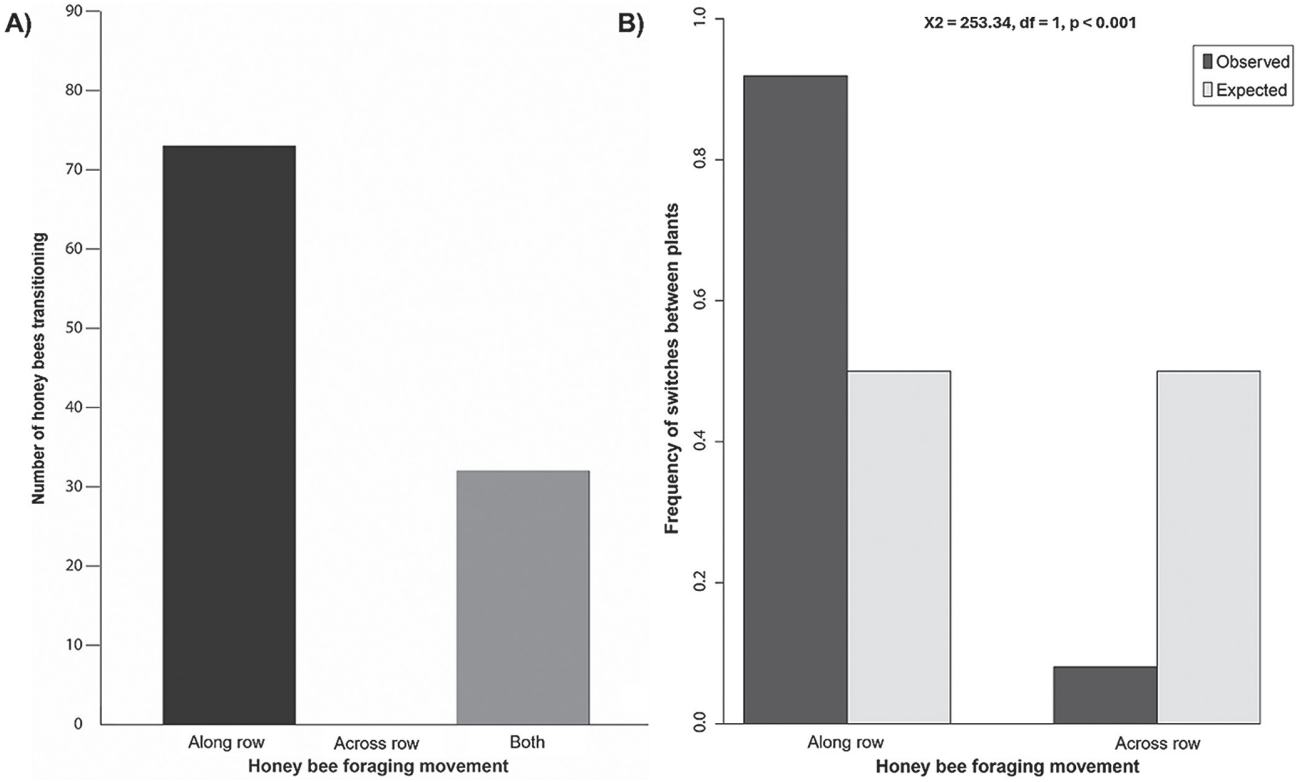

Figure 1: Honey bee movement in blueberry orchards. (A) Number of honey bees switching along, across, or both during an observation. (B) Frequencies of along-row and across-row movements when bees switched plants. If foraging were random, 50% of movements would occur across and 50% along rows (expected frequency = 0.5).

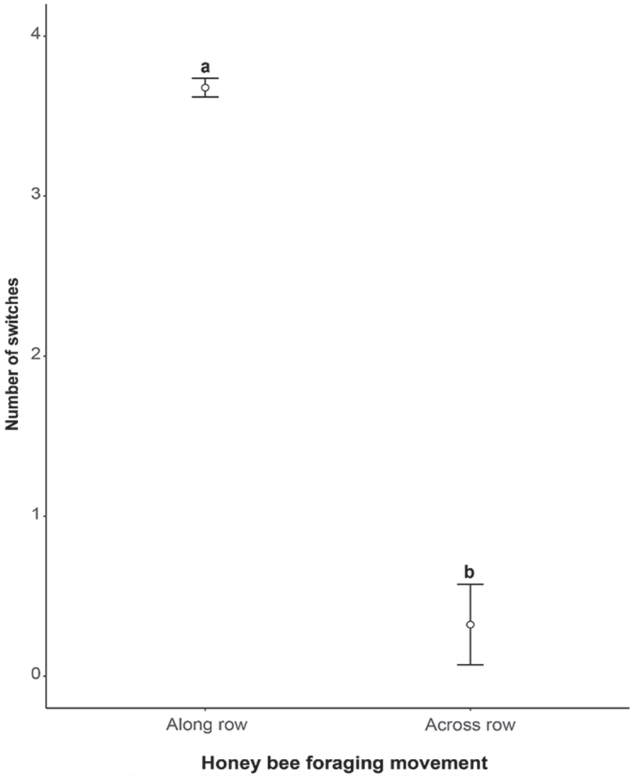

Figure 2: Average number of transitions between plants along or across rows during a honey bee foraging trip. Different letters indicate significance ($p < 0.05$) of linear contrasts (Tukey HSD). Error bars indicate standard error.

rows. Consequently, if donor cultivars and recipient cultivars are alternated by rows (a common occurrence on commercial farms), most pollen movement occurs within the same cultivar, leading to limited cross-pollination. This is problematic as cross-pollination with pollen from different cultivars generally increases fruit mass and diameter (MacKenzie 1997; Isaacs & Kirk 2010; Martin et al. 2025). Poor movement between rows of blueberries is a likely consequence of plant spacing differences as plants within a row generally overlap, while rows are separated by approximately 2.6 m, suggesting that, within similarly configured orchards, alternating rows of different cultivars may offer minimal improvement over solid-block plantings.

These results align with other studies suggesting that honey bees forage predominantly along rows and infrequently switch between rows (Free 1993; Delaplane et al. 2000). For example, Free and Spencer-Booth (1964) found that 89% of honey bees foraged along a row and only 11% switched across rows in an apple orchard, which has a similar spacing between plants to that of blueberries. While we found that 30% of honey bees switched between rows at some stage during a foraging bout, only 8% of transitions between plants occurred across rows. Other studies suggest that within-row foraging may occur because rows contain different cultivars, leading honey bees to show constancy or preference for a single cultivar (Free 1966; Kendall & Smith 1975; Gegear & Laverty 2004). However, this can be discounted in our study because all plants were the same cultivar. This leaves optimal foraging and differences in the distances of plants within and across rows as the most likely explanation for the foraging patterns observed in our study.

While our results document foraging behaviour, we can only infer what the effects on outcrossing are likely to be. Importantly, some outcrossing may occur when honey bees leaving their hive for subsequent foraging bouts carry pollen from plants previously visited by other bees owing to within-hive pollen transfer (DeGrandi-Hoffman et al. 1984). However, since pollen is quickly lost from pollinators while foraging (Minnaar & Anderson 2019), this pollen is only likely to have a positive effect at the start of a foraging bout. Notably, honey bees are notoriously efficient groomers (Amador et al. 2017; Nganso et al. 2017), suggesting that the beneficial effects of those infrequent transitions between rows

are unlikely to be very far-reaching. Studies of pollen carryover by bees for plant species that deposit much larger pollen loads per flower suggest that pollen movement typically does not extend beyond a small number of flowers. For example, *Sparaxis villosa* (Iridaceae) flowers deposited large pollen loads of about 130 grains per visit. However, after visiting 10 flowers, only 15% of that pollen was left on honey bee pollinators (Minnaar & Anderson 2019). This suggests that honey bees making rare transitions between cultivars will only visit a few flowers on the new cultivar before the pollen from the first cultivar is depleted. Similarly, when using fluorescent dye as a pollen surrogate, honey bees deposit the dye at an exponentially decreasing rate, with the first few flowers receiving most of it (Cresswell et al. 1995). In our study, transitions between plants (21%) are also interspersed with multiple transitions between flowers on the same plant (79%). This, combined with short pollen carryover distances, suggests that when a transition is made across a row, the pollen from across the row is unlikely to travel further than a few flowers on the next plant visited.

Although various studies, including this paper, have shown that honey bees tend to forage down blueberry rows and infrequently forage between rows, there is evidence that honey bees can switch frequently between rows of some cultivated species (Benachour & Louadi 2013; Kron et al. 2001). For example, when studying the two most cultivated plum species (*Prunus domestica* L. and *Prunus salicina* L.), honey bee flight patterns were most frequent between different rows (56%) (Benachour & Louadi 2013). Significantly, the distance between rows and between trees within the same row was equal (approximately 6 m).

We wish to highlight that studying foraging movement is an indirect assessment of pollen movement or plant mating in blueberries and therefore these results require careful interpretation. In addition, honey bee foraging behaviour is likely to be influenced by orchard-specific factors such as planting design, topography, and exposure to wind, which may vary among production systems. Nevertheless, these results point towards an urgent need for in-depth studies that directly assess the levels of intra- versus inter-cultivar pollen movement for crops that are reliant on inter-cultivar pollen transfer. Although molecular tools can assess outcrossing rates (Ferreira et al. 2010), one problem with these assessments is that they can only assess outcrossing rates for fruits and seeds that develop. Since intra-cultivar pollen movement often leads to fruit abortion, assessing outcrossing rates using developed seeds may lead to over-estimates of outcrossing (Anderson & Minnaar 2020). Perhaps the best way of assessing the actual effectiveness of planting alternating cultivars is to compare fruit yields of solid block plantings with fruit yields in blocks with alternating cultivars.

Although we only assessed the foraging movements of honey bees, we expect that the differences in planting distance between across versus along rows may have similar effects on the foraging movements of other insect pollinators such as native bees. Consequently, there is a need to study the foraging movements of other commercially important pollinators. Furthermore, we expect that similar foraging patterns may also be found in other crops where planting distances between rows are greater than planting distances within rows, suggesting a need to study this in other crops too.

To improve cross-pollination in highbush blueberries, we suggest alternating cultivars within rows rather than by rows. Such planting designs are likely to increase pollen transfer between cultivars without the need for alternative managed pollinators, which are not readily available in South Africa. Additionally, adjusting hive placement to encourage cross-row movement may help, although the most immediate improvement is likely through interplanting cultivars within rows.

In conclusion, this study demonstrates that row-restricted, optimal foraging behaviour by honey bees is likely to limit cross-cultivar movement in highbush blueberry production systems. These findings highlight that current row-based planting designs may constrain pollination efficiency, and that inter-row cultivar alternation alone is unlikely to substantially improve cross-pollination. Interplanting cultivars within rows represents a promising strategy to enhance pollen transfer and potentially improve fruit yield, laying the groundwork for future studies that directly measure reproductive outcomes. Future studies should replicate these observations across multiple farms and planting configurations to assess the broader applicability of these findings.

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