FISHING FOR FLIES: TESTING THE EFFICACY OF "STINK STATIONS" FOR PROMOTING BLOW FLIES AS POLLINATORS IN MANGO ORCHARDS

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Abstract—Pollinator communities are composed of diverse groups of insects, with radically different life histories and resource needs. Blow flies are known to visit a variety of economically important crop plants. Larval blow flies develop by feeding on decaying animals. Some fruit growers are known to place carrion on farms during the flowering season to attract adult blow flies (Calliphoridae). However, the efficacy of these "stink stations" has not been tested. We conducted a series of experiments to determine: 1) if stink stations promote the abundance of blow flies in mango orchards (*Mangifera indica* L.), 2) if any increases in the abundance of flies acts to promote pollination and fruit set in Australian mango orchards. Farms with stink stations had approximately three times more flies than control farms. However, the increased abundance of blow flies did not result in increased fruit set. Although stink stations increased the abundance of blow flies, we found no evidence that their use improves mango yield. This may be due to pollination saturation by a highly abundant native hover fly, *Mesembrius bengalensis* (Syrphidae), during our study. We hypothesize that stink stations may only be beneficial in years or regions where other pollinators are less abundant.

Keywords—Blow flies, Calliphoridae, Diptera, pollination, carrion, mango, hover fly, Syrphidae

INTRODUCTION

It has been well established that both wild and managed pollinators contribute to pollination services in agricultural ecosystems (Garibaldi et al. 2013; Rader et al. 2016, 2019; Potts et al. 2016; Willcox et al. 2019; Bernauer et al. 2022). Whilst managed pollinators are usually just a single species (e.g. *Apis mellifera,* L. 1758) (Potts et al. 2016), wild pollinator communities are often diverse assemblages of many species with unique life histories and habitat requirements (Herrera 1987; Larson et al. 2001; Potts et al. 2006; Woodcock et al. 2019). Diverse pollinator communities can have important benefits for agroecosystems, including reduced variability in pollination services between years (Blüthgen & Klein 2011; Senapathi et al. 2021) and more stable agricultural productivity (Klein et al. 2008; Albrecht et al. 2012; Garibaldi et al. 2016; Dainese et al. 2019). This is because species rich communities have higher ecological resilience, greater functional redundancy, and higher species complementarity (Memmott et al. 2004; Ives & Carpenter 2007; Kaiser-Bunbury et al. 2010; Bartomeus et al. 2013; Ellis et al. 2017; Winfree et al. 2018; Grab et al. 2019; Senapathi et al. 2021).

Efforts to conserve and increase pollinator diversity in agricultural landscapes have largely focussed on providing extra floral resources (Knop et al. 2006; Ekroos et al. 2014; Bartomeus et al. 2018). Annual flower strips (Feltham et al. 2015; Rundlöf et al. 2018) or perennial flowering plantings (Carvalheiro et al. 2012; Howlett et al. 2013) typically provide pollen and nectar to pollinators outside of crop flowering (Russo et al. 2013). Pollinators, including bees, have diverse nutritional needs that cannot usually be provided by a single crop plant (Sjödin 2007; Höcherl et al. 2012; Girard et al. 2012; Bukovinszky et al. 2017; Woodard & Jha 2017). As such, flower strips can support pollinator communities by complementing those resources provided by crop plants, as well as facilitating the movement of pollinators through the landscape (Dixon 2009). Extra floral resources have been shown to promote wild bee populations (Williams et al. 2015; Sutter et al. 2017; Kratschmer et al. 2019), as well as non-bee pollinators, like flies and butterflies (Aviron et al. 2011; Campbell et al. 2012; Korpela et al. 2013; Balzan et al. 2014), which can result in improved crop yields (Carvalheiro et al. 2012; Feltham et al. 2015; Rundlöf et al. 2018). However, wild pollinators often have diverse resource and habitat requirements that go beyond the provision of nectar and pollen (Rollin et al. 2013; Toivonen et al. 2022). Many non-bee pollinators have herbivorous, parasitic, predacious, and even saprophytic larval stages (Cook et al. 2020). For example, many common and important flower visiting hover flies (Syrphidae) have aquatic larvae that are associated with ponds and wetlands (Stewart et al. 2017). In crops that are mostly visited by non-bee pollinators, failure to consider the requirements of these other species may limit the benefit of providing extra floral resources (Toivonen et al. 2022). With our increased understanding of the importance of diverse pollinator communities, there is an increased need for management strategies that can promote pollinators with diverse life histories (Ssymank et al. 2008; Willcox et al. 2019; Cook et al. 2020).

Flies (Diptera) are the second most important pollinator group after bees (Ssymank et al. 2008; Rader et al. 2019). Flies make up a large proportion of all flower visitors in many agricultural systems (Ssymank et al. 2008; Orford et al. 2015; Rader et al. 2016; Toivonen et al. 2022) and can be as efficient as honey bees in depositing pollen (Rader et al. 2009; Howlett et al. 2017; Varun Rajan & Rami Reddy 2019). Like bees, adult flies visit flowers to obtain pollen and nectar (Ssymank et al. 2008). However, as most flies do not provision their offspring with resources, like bees, they may be more willing to visit less-rewarding flowers (Ssymank et al. 2008; Muñoz et al. 2021; Toivonen et al. 2022). Flies are often also very mobile, fecund and have short lifecycles, allowing their populations to adapt quickly to favourable environments (Rader et al. 2019). Flies often forage at different times of day and temperatures to bees (Ssymank et al. 2008), being more active in the early morning or during cold or rainy weather, as well as later in the flowering season (Ellis et al. 2017). Finally, non-bee pollinators have different patterns of movement within orchards than honey bees (Singh et al. unpublished), which tend to forage along linear features (Kobayashi et al. 2010; Mateos-Fierro 2020). As such, flies may be more likely to move pollen over greater distances and between adjacent varieties, thereby increasing the likelihood of cross pollination, which is important in many crops (Stern et al. 2004; Hudewenz et al. 2014; Gaffney et al. 2018).

Blow flies (Calliphoridae) are an important family of flower visiting flies (Orford et al. 2015; Rader et al. 2019; Willcox et al. 2019) and are common in pollinator communities, visiting a wide variety of plants, including many commercially important crop plants (Ssymank et al. 2008; Orford et al. 2015). As larvae, blow flies typically feed on rotting or necrotic animal tissues, whereas adults of many species of blow fly visit flowers to feed on pollen and nectar, which are important resources for growth and reproduction (Kearns 2002; Kevan 2002; Ssymank et al. 2008). Some blow flies have been commercially reared for use as managed pollinators (Howlett 2012), whilst many other species also have characteristics that are desirable as pollinators (Cook et al. 2020). Although blow flies are common in many pollinator communities, they generally make up only a small proportion of crop visitors (Singh et al. unpublished; Bernauer et al. 2022). For example, a single genus of blow fly (*Chrysomya*), makes up around 5% of all flower visits in avocado, mango and macadamia orchards in Australia (Willcox et al. 2019). Methods that increase the abundance of blow flies on farms could therefore help to create more species rich and stable pollinator communities (Loreau et al. 2001; Hooper et al. 2005; Orford et al. 2015).

In tropical regions worldwide, mango (*Mangifera indica* L., Anacardiaciae) is well known to be visited, and potentially pollinated by, blow flies (Ramírez & Davenport 2016). In a previous study of mango pollinators in Malaysia, *Chrysomya* spp. (Robineau-Desvoidy, 1830) blow flies were the most frequent visitors to inflorescences and carried on average around 2500 mango pollen grains per fly (Huda et al. 2015). The presence of blow flies on mango trees and flowers has not gone unnoticed by mango growers (JF, personal

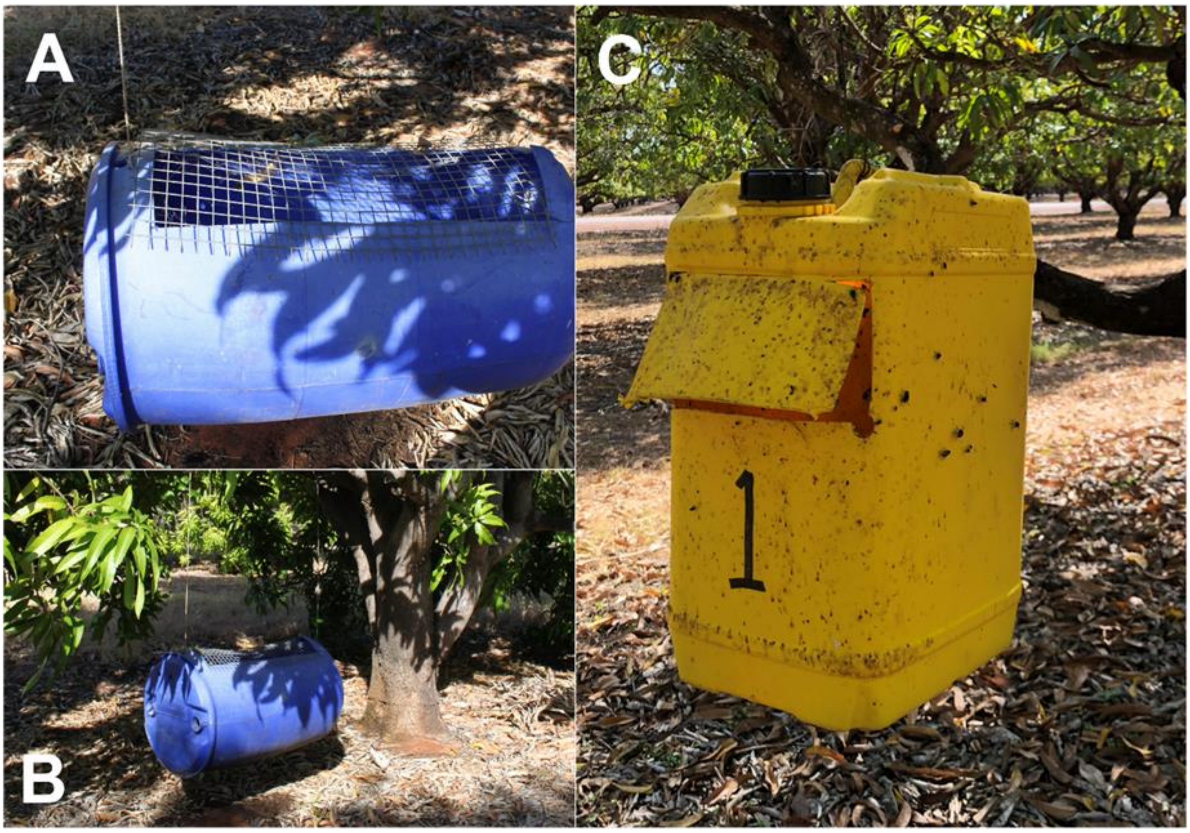

Figure 1. Typical designs of "stink stations" used by growers in the A-B) Katherine and C) Darwin mango growing regions of the Northern Territory, Australia. Stations are usually constructed from recycled chemical containers of varying sizes (20-250 L) and suspended from mango trees to avoid competition from ants. Steel mesh coverings are sometimes added to facilitate access by blow flies and prevent scavenging by vertebrates.

observation). The preference of blow flies for carrion is also well known, particularly in the tropics, where animal tissues putrefy and become "fly-blown" extremely quickly. Indeed, the synanthropic tendencies of blow flies to congregate around humans and our waste has made them one of the most widely recognized off all insect groups (Marshall 2012), being colloquially referred to as "blowies" or even "dunny budgies" in Australia's Northern Territory. Perhaps because of these two common observations, mango farmers in Northern Australia have been known to create "stink stations" (Fig. 1) by placing carrion beneath mango trees to attract blow flies into orchards to act as pollinators. This practice has been used for decades and the authors have also heard anecdotal reports of similar practices occurring in rambutan crops in Australia, as well as avocado in Peru (JF, personal observation). In Australia, commercial products are even available for the purpose of promoting blow fly populations in avocado orchards (Australian Tree Crop 2020, 2022), whilst patents have been applied to copyright similar methods in China (何寒 2012). However, such methods have never been adequately tested.

Several studies have trialled various baits for encouraging flies into mango orchards, including rotting meat and animal excrement (Sharma et al. 1998; Alqarni et al. 2017; Yadav et al. 2018). These studies found that some baits are highly attractive to blow flies. However, no studies have quantified the effect of these baits or stink stations on fly abundance compared to control farms or assessed the subsequent effects on visitation on fruit set. This is further complicated by the many and varied methods for creating and deploying baits for flies, that range from whole animal carcases to manure heaps and even emulsions of fish oils that are sprayed into crop canopies (JF, personal communication).

To address this lack of understanding, we conducted a series of experiments to determine: 1) if stink stations baited with carrion increase the abundance of blow flies in mango orchards 2) if the increased abundance of flies acts to promote pollination and fruit set in Australian mango orchards. In undertaking this study, we hoped to promote the use of alternative pollinators in horticulture and identify new methods of promoting pollinator diversity and abundance.

MATERIALS AND METHODS

MANGO ORCHARDS AND TREES

The study was carried out in the Darwin, NT (12.4° S, 130 ° E), Katherine, NT (14.4° S, 132.2° E) and Burdekin, QLD (19.5° S, 147.4°) mango growing regions of Australia. Mango farms in these regions predominantly grow the "R2E2" and "Kensington Pride" varieties, Kensington Pride being the most widely grown variety in Australia (Department of Agriculture and Fisheries 2022). All farms were managed conventionally, using synthetic insecticides and fertilisers and drip-irrigation systems. In the Darwin and Katherine regions, the majority of mango trees flower between May and July, whilst flowering in Burdekin occurs primarily in August.

During flowering, mango trees bare up to 3000 inflorescences, known as panicles, with each panicle bearing hundreds to thousands of individual flowers (Mukherjee 1953; Free 1973; McGregor 1976). Flowers can be either perfect (staminate and pistilate) or purely male (staminate only). The proportion of perfect to male flowers varies widely in response to both endogenous (e.g., tree age and size) and environmental factors (e.g., rainfall, humidity and temperature) (Davenport 2009; Ramírez & Davenport 2016). Nectar is produced in small amounts from a fleshy disk located below the single ovule.

Pollination is critical for mango fruit development to occur, as unfertilised flowers typically abscise shortly after flowering (Ramírez & Davenport 2010, 2016). Evidence for the importance of cross-pollination in mangoes is mixed. Insects are believed to be important for fruit set with several experiments showing low or no fruit set when insect pollinators are excluded (Ramírez & Davenport 2016). Some varieties appear to benefit strongly from cross-pollination (Dag et al. 1997, 2009), whilst in other varieties self-pollination, via wind or gravity, appears to be common (Sousa et al. 2010; Ramírez & Davenport 2016). At the time of writing, there is no published data on the importance of cross-pollination in Kensington Pride. However, experiments to determine the importance of cross-pollination in this variety are underway (Dr James Makinson, personal communication).

STINK STATIONS AND FLOWER VISITATION

We conducted an experiment to test if stink stations increase the abundance of flies, and consequently fruit set, on mango farms in the Darwin region in June 2021. To do this, we deployed stations on three experimental farms and compared with this against three control farms. Farms with stink stations were selected to be at least 10 km from control farms to reduce the likelihood of experimental farms influencing control farms. Only one farm, farm JK, had six small honey bee hives (*Apis mellifera*) present on the property during flowering. A single managed stingless bee hive (*Tetragonula mellipes* Friese 1898) was present on farm LL throughout flowering but many wild colonies were present in the surrounding woodlands.

On experimental and control farms, we selected 10 rows of trees across the orchard that were at least 100 m apart. Because tree crop variety can play an important role in pollinator preference (Stelinski et al. 2018), we used the same variety of mango, Kensington Pride, across all farms. Where possible, rows were selected prior to our first visit by row number (i.e., row number 10,20,30). However, flowering within rows was often inconsistent, with many trees within a row producing few or no flowers. As such, some pre-selected rows were excluded and other nearby rows with sufficient flowering were used instead. Trees within rows were selected haphazardly but were always at least five trees from the orchard edge and had at least five flowering panicles.

On experimental farms, one tree in each row received a stink station. Stink stations were constructed following the methods generally used by growers, although practices vary between individuals and regions. The containers were usually a re-purposed 20 L insecticide or fertiliser bottle (Fig. 1C), that had been washed thoroughly (i.e. at least three times) and cut open along the top or side to allow carrion bait to be placed inside. For each stink station, ~2 kg of carrion (whole fish or chicken carcasses) was placed within each container, as well as 1 L of water to prevent the carrion from drying out. These containers were then placed in a shaded position under the trees at the beginning of flowering. The stations were refreshed with another 2 kg of carrion and 1 L of water after 21 days. This was based upon the estimation that at an average temperature in Darwin of ~25°, the most numerous genera of blow fly in northern Australia (*Chrysomya spp*.) would complete their lifecycle in around 12 days (Byrd & Butler 1997; Zhang et al. 2019) and begin egg laying after another 5-7 days (Gabre et al. 2005; Hadura et al. 2018).

We were also interested in determining if trees near to the stink stations, not just those directly next to them, benefit from the presence of stink stations. As such, for each station we selected two nearby trees within each row at distances of 10-30 m and 30-50 m for pollination surveys (Fig. 2). The distance between trees was measured as the distance between trunks. The distances to the station varied due to the spacing of trees within the orchard, as well as the distribution of flowering trees within each row.

On the three control farms, three trees were selected on ten rows that were at least 100 m apart, giving an equal number of trees on control and experimental farms (*N* = 90). In each row, trees were selected haphazardly to be in the middle of the row, at least 20 m apart and with at least five flowering panicles.

To determine if the stink stations promoted blow fly abundance compared to control farms, we conducted pollinator surveys on all selected trees on both the experimental and control farms. Surveys were conducted twice, at 9-11 am and 2-4 pm, for each tree on two non-consecutive days during flowering. Future studies, however, should be aware that recent research has determined that blow flies are most active in the early morning (8-9 am), and late afternoon (5-6 pm) (Singh et al. unpublished). Surveys were not conducted during periods of rainfall or high cloud cover, which occurred for just two days in mid-June. For each survey, we slowly walked around each tree for three minutes and observed all panicles within 3 m of ground level (i.e. those that we could accurately observe), which accounted for 50-75% of the flowers on each tree. The abundance and identity of all insects contacting the flowers was recorded (Fig. 2).

One additional farm (PT) was originally intended to be used in our test of stink stations. However, stations on this farm failed to be visited and colonised by flies. This was most likely

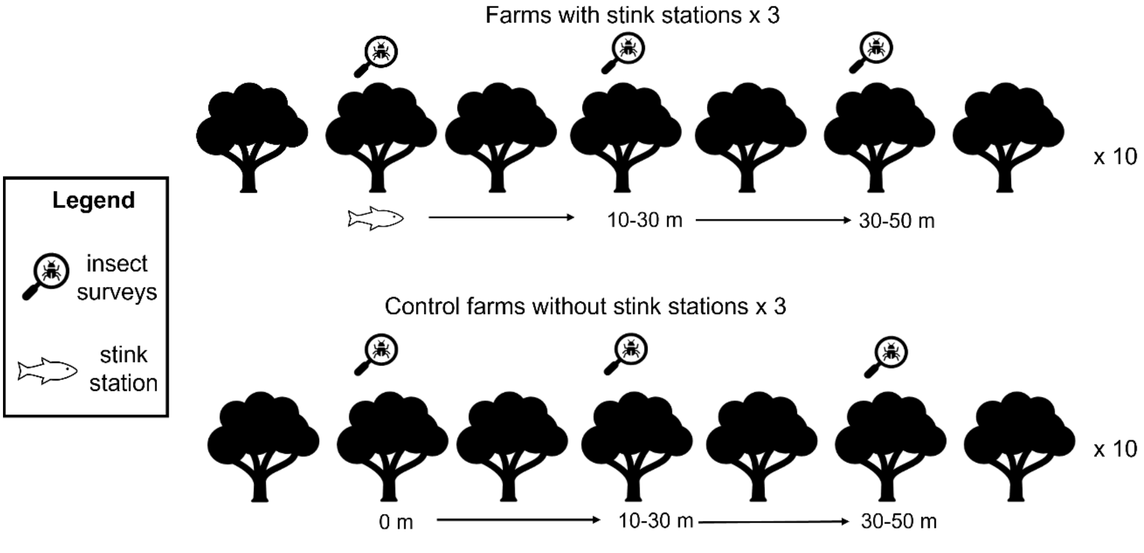

Figure 2. Design of experiment to test the effect of stink stations on blow fly visitation to mango trees and effective spatial scale. Six farms were used in total, three farms received stink stations and three received no stink stations (control). Control farms were at least 10 km from farms with stink stations. Stink stations were placed under 10 trees in randomly chosen rows at least 100 m apart. Pollinator surveys were conducted at the stink station and at increasing distances from the stink station within each row (0, 10-30 and 30-50 m). An equal number of insect surveys were conducted on trees on control farms.

due to the frequent use of broad-spectrum insecticide sprays (Dimethoate 30 EC) on the farm during peak pollinator activity in the late afternoon (Singh et al. unpublished). After spraying, many dead maggots and adult flies were observed inside the stink stations, suggesting they had been killed by insecticide exposure. Although this farm was not included in our test of stink stations, we continued to survey this farm for pollinator activity and fruit set, using the same methods as described above.

Visual inspection of the data indicated that the number of blow fly visits to panicles on farms with and without stink stations was not normally distributed. As such, we used a non-parametric Kruskal-Wallis rank sum test in the Stats package (R Core Team, 2021) to test if trees on farms with stink stations had a greater number of blow flies visiting flower panicles. We also used a Kruskal-Wallis test to determine how the abundance of blow flies per tree changed with increasing distance from the stink stations. We used Wilcoxon rank sum tests in the Stats package (R Core Team, 2021) to perform pairwise post-hoc comparisons between distances.

FRUIT SET

To determine the effect of stink stations on fruit set we conducted surveys of fruiting using the same experimental set up described above. We selected five unopened panicles on each tree (*N* = 210) on the seven farms (including farm PT) prior to the beginning of our pollinator surveys. Selected panicles were no higher than 3 m from ground level and, where possible, were selected on both sides of the tree row to avoid any biases due to abiotic conditions. Early fruit set surveys were conducted exactly 28 days after the first pollination survey. For each tree, we counted the total number of early fruits developing across the five tagged panicles. In mango, many panicles produce small "pea-sized" unfertilised fruits (known colloquially as "nubbins") that are aborted soon after flowering finishes. Because of this, early fruit set is likely to be significantly greater than the number of fruits that reach maturity. As such, on all farms we also counted late fruit set on the 5th of August (~6 weeks after flowering), which was the latest possible date for fieldwork. For late fruit set, we only counted the number of fruits greater than 30 mm and in which the connective tissue between the fruit and panicle had reddened in colour, indicting the fruit would be held to maturity (Darren Hill, Cheeky Farms, personal communication). In addition, we gently tapped all remaining panicles to remove any fruit that was likely to be aborted.

Both early fruit set and late fruit set were analysed using generalised linear models (GLM's) using the *Stats* package (R Core Team 2021) in R studio (RStudio Team 2020). We used the *descdist* function in the R package *fitdistplus* (Delignette-Muller & Dutang 2015) to create Cullen and Frey plots and used these to visually determine the correct error distribution for the dependant variables (i.e. early and late fruit set). Where two error distributions appeared closely matched (i.e. Poisson and negative binomial), we constructed both models and then compared them using likelihood ratio tests in the *lmtest* package (Zeileis and Hothorn 2002), preferring the model with the lowest log-likelihood. In all cases, the Poisson error distribution provided the best fit to the data.

GLM's were used to model the effect of the independent variables, the presence of stink stations and distance to stink stations, on early and late fruit set at the tree level (*N* = 210). In addition, we also used GLM's to test the effect of the non-blow fly pollinators on fruit set. To do this we calculated the total numbers of the two most abundant non-blow fly flower visitors, *Mesembrius bengalensis* (Wiedemann 1819) and *Tetragonula spp.* (Moure, 1961) that we observed for each tree, as well as the total number of insect visits for each tree, and modelled early and late fruit set as a function of these as independent variables. The correct error distributions were determined using the method described above.

FLY TRAPPING

To determine if the stink stations increased blow fly abundance on mango farms in Darwin in 2021, we surveyed blow flies on six farms using Envirosafe Fly Traps (Evergreen Marketing, Malaga, WA). Trapping was conducted twice at each farm exactly 14 and 28 days after the initial deployment of the stink stations. Each farm (n=3) with stink stations was paired with a control farm more than 10 km away which had fly traps deployed at the same time. The traps were prepared according to the manufacturer's instructions; each trap received 1 sachet of

Envirosafe Eco-Bait and was then filled to 1/3 full of water. Four traps were placed on each farm in a 250 x 250 m square configuration. Traps were hung from branches at approximately 1.75 m above the ground, positioned to be shaded throughout the day, and left for exactly 72 hours before being collected and then frozen to kill any flies and maggots alive in the traps. The traps were then defrosted and the number of flies in each trap counted. We used a two-way ANOVA in the R *Stats* package (R Core Team, 2021) to test for the effect on stink stations, date of trapping and their interactions on the number of blow flies caught.

POLLINATION EFFICIENCY

To determine if the blow flies around the stink stations move and deposit pollen, we assessed pollen deposition by blow flies during flower visits, as well as other flower visiting insects around the orchard. Pollen deposition was studied on farms in all three mango growing regions – Darwin, Katherine and Burdekin. Pollen deposition was studied on farms in Katherine and Burdekin in the flowering season of July and August 2019, respectively. Pollen deposition was studied in Darwin in July 2021, using the experimental set up described above.

On each farm, 12-24 unopened panicles were fitted with BugDorm Insect Rearing Sleeves (L70 x W30 cm), (Megaview Science Co., Ltd, Taiwan) to prevent insect visitation. After 2-5 days, the panicles were removed from the trees with secateurs and placed upright 1-3 m from a stink station that had been set up for 4-10 days. Stink stations were constructed as described above. The bags were then removed to allow insects to visit the flowers. Most insects visited several flowers on each panicle before departing, however, some insects returned to a flower that they had previously visited on the same panicle (up to four times). The number of visits to each flower was recorded. After the insect had left the panicle, the visited flowers were removed with forceps and stored on ice in a 1.5 ml centrifuge tube.

A sub-sample of flies were collected for species identification. We used a general key for the identification of Diptera to identify blow flies from other families of Diptera known to breed in carrion (Marshall 2012). No key is currently available for the identification of blow flies in Northern Australia. As such, identification was performed by JF using entomological keys for the identification of blow flies in Southern Australia (Wallman 2001), which is the most appropriate key at the time of writing. *Chrysomya rufifacies* (MACQUART 1842) and *C. saffranea* (BIGOT 1877) were commonly collected around stink stations but could not be reliably identified by the naked eye during single visits, so were grouped for analysis. The stingless bee, *T. mellipes*, often visited panicles positioned near stink stations resulting in 43 flower visits, however, we recorded no visits from *M. bengalnesis* despite their high abundance.

Pollen deposition might also occur through pollen moving within bags due to the action of gravity or wind. As such, an approximately equal number of control flowers, that had not been visited, were removed from the panicles each day. Visited and control flowers were taken back to the lab where each stigma was removed and placed on a microscope slide. The stigmas were then suspended in clear nail varnish and gently compressed under a glass cover slip. After the varnish had dried and the stigma was fixed in place, the number of mango pollen grains deposited by each visitor was counted using a Leica EZ4 stereo microscope (Leica-Microsystems, Wetzlar, Germany). We used a Dunnett's Test in the R package DescTools (Signorell et. al. 2021) to perform pairwise comparisons between treatment groups and control stigmas. We used a Kruskal-Wallace test to determine if the number of visits to each stigma influences pollen deposition.

RESULTS

STINKS STATIONS AND FLOWER VISITATION

Across all farms in the Darwin region, the highest percentage of visits (55 %) was made by a large hover fly, *Mesembrius bengalensis*. Stingless bees (*Tetragonula* spp.) also made a high proportion of all visits (16%), but mostly on farms without stink stations (Fig. 3A). In contrast, European honey bees (*Apis mellifera*) were rare and accounted for less than 1% of all visits.

Farms with stink stations had a much higher percentage of visits by blow flies (34%) than farms without (3 %) (Fig. 3B). The number of blow flies visiting panicles on farms with stink stations was significantly higher than on farms without (Kruskal-Wallis $\chi^2 = 168.52$, df = 1, $P < 0.0001$).

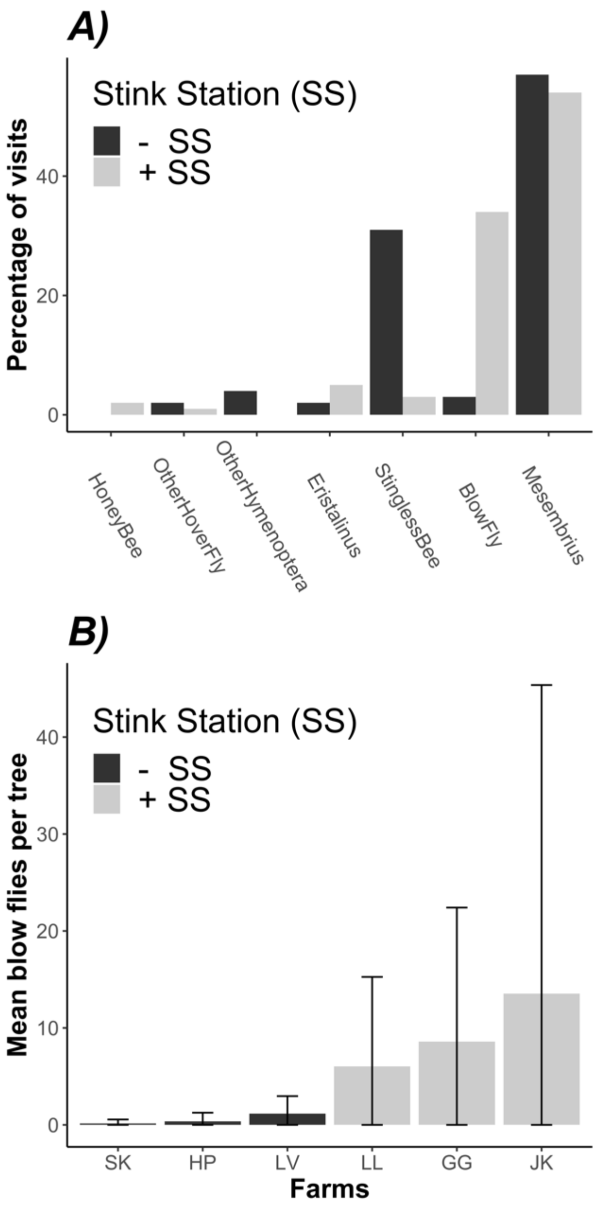

Figure 3. A) Flower visitors by percentage of total visits to mango panicles on farms with (N = 3) and without stink stations (N = 3) in Darwin, NT, Australia. B) Mean number of blow flies observed per tree (summed across pollinator surveys) on farms with and without stink stations during three-minute observation periods. Error bars show the standard deviation of the mean.

There was a significant decrease in the abundance of blow flies with increasing distance from stations (Kruskal-Wallis $\chi^2 = 99.16$, df = 3, $P < 0.0001$). Post-hoc pairwise comparisons revealed there were significantly more flies at trees next to stink stations (0-10 m) compared to trees at 10-30 and 30-50 m from the stink stations ($p < 0.0001$) (Fig. 4). There was no difference in the number offlies recorded between trees at 10-30 m and 30-50 m ($P > 0.05$). However, blow fly abundance on trees 10-50 m from stink stations was still significantly greater than on control farms, indicating that stink stations do promote blow fly abundance at distances of at least 50 m in mango orchards.

FRUIT SET

Early fruit set on farms with stink stations was not significantly different from farms without stink stations (Est. = -0.012, SE = 0.008, T = -1.43, P = 0.152) (Fig. 5A). In addition, early fruit set on trees closer to stink stations was not significantly different from trees further away from stink stations, or on control farms (Est. = 0.0001, SE = 0.0001, T = 1.265, P = 0.208) (Fig. 5C).

Late fruit set on farms with stink stations was not significantly different from farms without stink stations (Est. = -0.19, SE = 0.113, T = -1.757, P = 0.0789) (Fig. 5B). Late fruit set on trees closer to stink stations was not significantly different from trees further away from stink stations, or on control farms (Est. = 0.002, SE = 0.001, T = 1.603, P = 0.109) (Fig. 5D). Both late and early fruit set were lowest on farm PT, where high pesticide application rates likely resulted in very low pollinator activity (JF, personal observation).

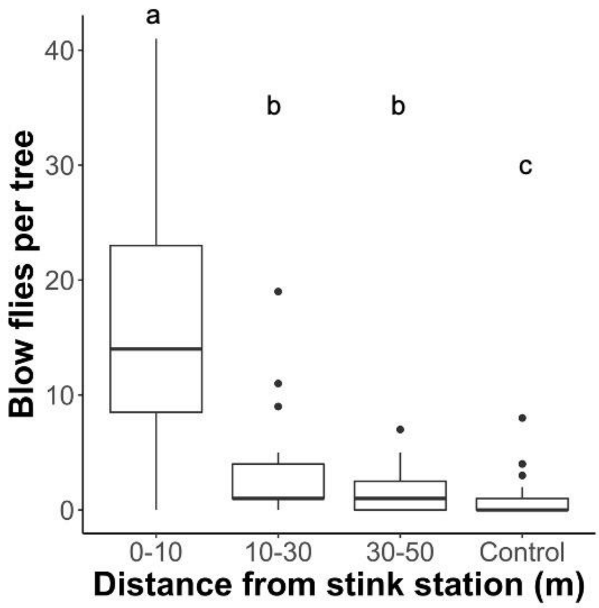

Figure 4. Mean numbers of blow flies observed per tree during three-minute pollinator surveys at increasing distances from stink stations on mango farms around Darwin, NT, Australia. Trees on control farms were at least 10 km from farms with stink stations. Stink stations were at least 100 m apart on experimental farms. Boxes with a common letter are not significantly different.

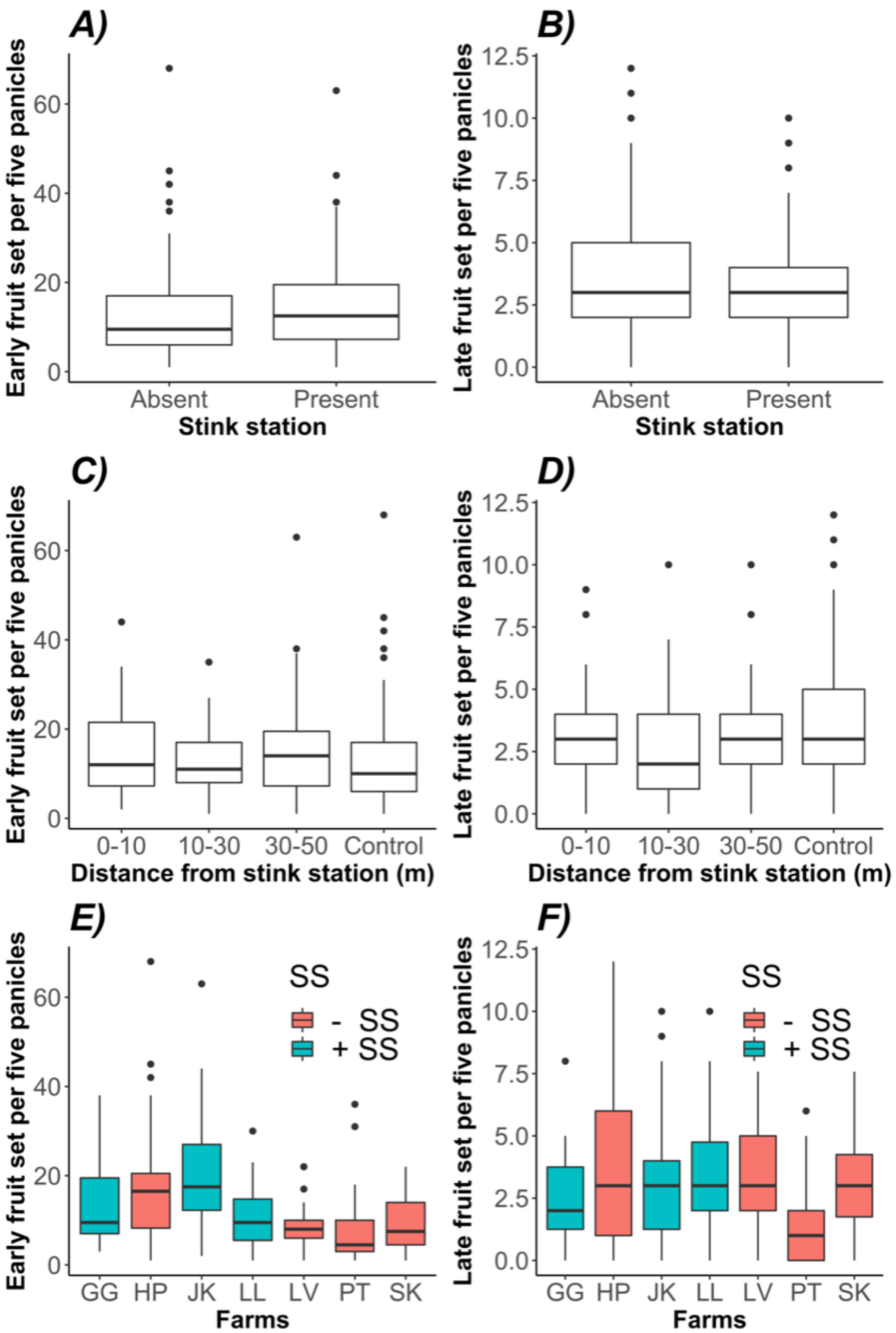

Figure 5. Mean fruit set per five panicles on trees (*N* = 210) on seven mango farms around Darwin, NT, Australia. Fruit set is divided into the early (left side) (5-30 mm diameter) and late stages (right side) (> 30 mm diameter). A-B) Comparison of median early and late fruit set on farms with and without stink stations. C-D) Comparison of median early and late fruit set on farms at increasing distances from stink stations. E-F) Median early and late fruit set across all farms with and without stink stations.

Early fruit set was significantly predicted by the total number of *Mesembrius bengalensis* hover flies observed visiting each tree, but not by the presence or distance to stink stations (Table 1). In contrast, total insect visits per tree and total visits by stingless bees (*Tetragonula mellipes*) did not significantly predict early fruit set (Table 1) across the seven surveyed farms. In contrast to early fruit set, late fruit set was not significantly predicted by total visits by hover flies, stingless bees or all insect visits per tree ($P > 0.05$).

Early fruit set was much more variable at the farm level than late fruit set (Fig. 5E-F). Median values for late fruit set were remarkably similar across most farms compared to early fruit set, suggesting an upper limit to the number of fruits that can mature per panicle. Nevertheless, early fruit set per panicle was still a significant predictor of late fruit set, suggesting that early fruit set plays a significant role in the final number of mature fruits per panicle (Est. = 0.03, SE = 0.004, z = 6.8, $P < 0.0001$).

Table 1. Coefficient estimates for the effect of number of visits by the two most common flower visitors and total insect visits observed per tree on early fruit set in mango trees (*N* = 210) In the Darwin growing region in 2021. Results were obtained using a generalised linear model with a Poisson error distribution.

	Est.	SE	T	*P*
(Intercept)	0.079	0.004	17.626	> 0.001*
Mesembrius	0.012	0.005	2.045	0.042*
Stingless Bee	0.001	0.004	0.383	0.702
Total insect visits	0.001	0.002	-0.970	0.333

FLY TRAPPING

The presence of stink stations had a significant positive effect on the number of blow flies caught in Envirosafe Fly Traps (F = 7.92, df =3, *P* = 0.007). The mean number of blow flies caught on farms with stink stations was more than three times higher than farms without stink stations (Fig. 6). This was true of both the first and second trapping periods. However, variance in trap catches on farms with stink stations was almost ten times greater (var = 85,023) than farms without stink stations (var = 9,791). Significantly fewer flies were caught during the second sampling period compared to the first (F = 5.17, df = 3, *P* = 0.028), regardless of the presence of stink stations (F = 0.976, df = 3, *P* = 0.32), indicating that other external factors may explain the decline in the number of blow flies caught.

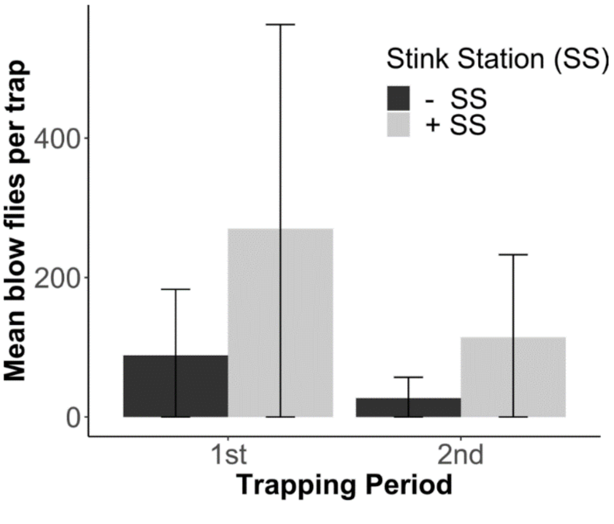

Figure 6. Mean number of blow flies caught in Envirosafe Fly Traps on mango orchards with and without stink stations across six farms around Darwin, NT. Error bars show the standard deviation of the mean. Four traps were deployed per farm for a period of 72 hours. Traps were deployed twice on all farms with an interval of two weeks.

POLLINATION EFFICIENCY

Pollen deposition after single insect visits to stigmas was extremely variable, with most visits (181/282 = 64%) resulting in no transfer of pollen. Meanwhile, the remaining 101 visits resulted in the transfer of between 1 and 179 pollen grains.

The number of pollen grains on insect-visited stigmas was not significantly different to unvisited control stigmas (*P* > 0.05), for all types/species of flower visitor (Fig. 7). Of 231 control stigmas, 188 (81%) had no pollen grains attached, while the remaining 43 control stigmas had between 1 and 43 pollen grains.

In our study, 261 stigmas received just one visit, 13 stigmas received two visits, five stigmas received three visits and just three stigmas received four or more visits. Multiple visits had a significant positive effect on pollen deposition per stigma (Kruskal-Wallis χ^2 = 29.37, df = 6, $P < 0.0001$).

DISCUSSION

We set out to investigate if stink stations can promote blow fly abundance and thereby pollination and fruit set in Australian mango farms. We found that farms with stink stations had approximately three times more flies than control farms. Furthermore, significantly more flies were present on mango panicles around stink stations. This increase in fly abundance persisted at distances of at least 50 m relative to control farms. Blow flies also deposited similar amounts of pollen on mango stigmas as stingless bees. Despite this, the increased abundance of blow flies did not result in increases in early or late fruit set. As such, although stink stations successfully increased the abundance of blow flies, we found no evidence that their use promotes yields in Australian mango farms.

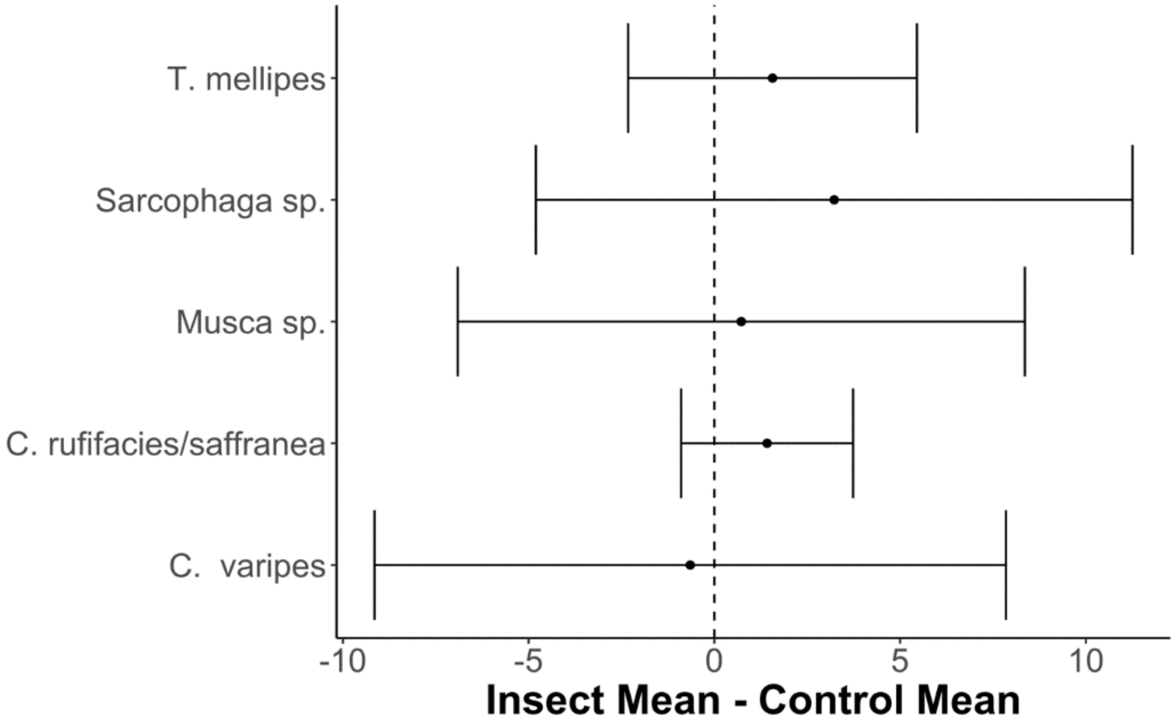

Figure 7. Mean difference between the number of mango pollen grains on stigmas collected after single visits by insects around stink stations vs the number of pollen grains on unvisited control stigmas (dashed line). Error bars show 95% confidence intervals. Visiting insects included *Chrysomya rufifacies/saffranea* (*N* = 189), *Chrysomya varipes* (*N* = 8), *Musca* spp. (*N* = 10), *Sarcophaga* spp. (*N* = 9), *Tetragonula mellipes* (*N* = 43). Control stigmas = 231. *Chrysomya rufifacies* and *Chrysomya saffranea* were both commonly collected around stink stations but could not be reliably identified by the naked eye during single visits and were grouped for analysis.

THE ROLE OF NON-BLOW FLY POLLINATORS

It is interesting to consider why an increase in the abundance of blow flies did not result in a corresponding increase in fruit set. We believe that any positive effect of stink stations on fruit set may have been negated by the high abundance of other pollinators, resulting in pollination saturation. In particular, the near ubiquitous presence of *Mesembrius bengalensis* hover flies across nearly all trees and farms is likely to have had a significant impact on the outcome of experiment (Fig. 3A). In our pollinator surveys, we observed up to 60 *Mesembrius bengalensis* hover flies per tree in a single three-minute observation period (mean = 3.3, SD = 5.6). Two of seven collected female *M. bengalensis* had large, developed ovaries, suggesting that at least some individuals were breeding during mango flowering and all collected females had large amounts of mango pollen in their guts (JF, data unpublished). Our modelling of *M. bengalensis* abundance also revealed a significant positive association with early fruit set, but not late fruit set (Table 1).

Data from other studies suggests that the abundance of *M. bengalensis* hover flies during the flowering season of 2021 was significantly higher than in previous years (Singh et al. unpublished). Why the change in abundance occurred is not known but may relate to higher rainfall in the preceding monsoon season. Although the larval habitat of *M. bengalensis* is not currently known, it is likely that they breed in freshwater habitats. Close relatives of these hover flies breed in wetlands, where they filter feed on bacteria and other microorganisms (Perez-Banon et al. 2013). The Darwin region is surrounded by a vast network of seasonal wetlands (Whitehead et al. 1990). The strong wet season experienced in 2020-2021 may have substantially increased the amount of available habitat for *M. bengalensis*, resulting in their high abundance during the mango flowering season of 2021. Monsoon seasons show substantial variation in total rainfall in Northern Australia (Kajikawa et al. 2010; Wang et al. 2014), so in drier years the abundance of *M. bengalensis* may be lower and consequently both pollination and fruit set may be reduced compared to 2021. For this reason, we believe it is possible that stink stations may prove more effective in drier years, or in any other situation in which the abundance of other pollinators is reduced. Further research on both the inter-annual variability of wild mango pollinator populations (Kremen et al. 2002; Willcox et al. 2019) and the effectiveness of stink stations is required to address these questions.

A native stingless bee, *Tetragonula mellipes,* was also a common visitor on mango farms and could also have negated any positive effects of stink stations on fruit set. Indeed, stingless bees have been reported to be a common and effective pollinator in Australian mango orchards (Willcox et al. 2019). Our modelling found no association between the abundance of stingless bees and fruit set in our study. This may be because stingless bees were not present on many farms where high fruit set was observed. However, it is likely that stingless bees are significant pollinators on some farms (Willcox et al. 2019) but their beneficial effects may have been masked by the ubiquitous presence of *Mesembrius* hover flies, which were present across all high yielding farms.

Stingless bees were most common on control farms (Fig. 3A) but why this occurred is unclear. All farms were conventionally managed and were situated in similar habitats; native grassy woodlands comprised of eucalyptus dominated plant communities (JF, personal observation), which presumably offer similar nesting habitat and floral resources for stingless bees. As such, there is no obvious reason for differences in stingless bee abundance, but it is possible that some undetermined environmental factor may explain the observed patterns (i.e. fire history). Alternatively, it may be that the higher activity of blow flies on experimental farms could have negatively impacted on stingless bee activity on farms with stink stations. Male blow flies are known to take up perches on leaves and sticks near carrion and chase any passing object that resembles a female (Trischler et al. 2010; Butterworth et al. 2019). These amorous behaviours may have deterred stingless bees from the mango trees near carrion. Determining if these mating behaviours do impact on other pollinators will be important in our understanding of blow flies as potential crop pollinators in mixed species assemblages.

POLLEN EFFICIENCY

In our study, we quantified the pollen deposited by blow flies on mango stigmas. Approximately 65% of visits did not result in pollen transfer. Low rates of pollen transfer are not unusual, with previous studies estimating that only 2 in 3 visits from bees result in pollen transfer and only 1 in 5 visits in flies (Herrera 1987). Variance in the number of pollen grains deposited on control stigmas was also extremely high (0-179). Previous studies have found that blow flies can carry an average of ~2500 (SE = 500) mango pollen grains (Huda et al. 2015). However, actual pollen deposition during visits is likely to be related to a range of factors including pollen carrying load, time spent per flower and the likelihood of stigmal contact (Rader et al. 2009; Woodcock et al. 2013; Bernauer et al. 2022). In at least some crops, multiple visits are required to maximise fruit set (Kendall et al. 2020). Our data also support this as multiple blow fly visits were found to significantly increase the number of pollen grains deposited per stigma. As such, it seems that because the mean number of grains deposited by each visit is often very low, successive visits may be required for successful pollen deposition.

Likely because of the high variance in pollen deposition, and because many control stigmas were found to have pollen grains on them, no insect visitors deposited significantly more pollen than control stigmas. How pollen became deposited on the control stigmas is unknown but could be related to a range of abiotic factors including wind, gravity (Mallik 1957; Free & Williams 1976) or possibly the activity of very small insects within the bags (Ananthakrishnan 1993; Ramírez & Davenport 2016). During our study no insects were observed to be foraging within the bags or through the bags prior to their removal from the trees. As such, we believe that a high proportion of pollen on the control stigmas can be explained by the movement of pollen within the pollinator exclusion bags by abiotic factors, and possibly as the result of friction by the bags themselves. What proportion of fruit set is accounted for by abiotic pollination in Kensington Pride remains to be determined.

FRUIT SET

Fruit set in orchards can be limited by a variety of factors including resource allocation and pollen deposition, both in terms of pollen quantity and quality (i.e. proportion outcrossed pollen) (Mashood Aliyu 2008; Subbaiah 2022). The metric that we used to measure fruit set was the number of fruits per five panicles, as accurately counting fruit set at the whole tree level is impractical when working with large numbers of trees and with tall trees. The median number of large fruits was remarkably similar across farms (Fig. 5), suggesting that fruit set may have been maximised in many studied panicles. Upper limits on fruit set have been documented in other tree crops, where local resource limitation in individual shoots prevents flowers from developing (Lampinen et al. 2011; Cunningham et al. 2019). This may also explain why our modelling found differences in the predictors of early vs late fruit set. Most early fruits are typically aborted, and their abundance may be more dependent on successful pollination and ovule fertilisation than resource limitations. Estimating whole tree fruit set using machine learning may give greater resolution in future studies of tree crop pollination (Payne et al. 2014; Anderson et al. 2019). Studies of the interactions between pollen and resource limitation in mango will also be important for determining how to maximise fruit production. As stated in the methods, the requirement of the Kensington Pride variety for cross-pollination is yet to be determined.

BLOW FLIES ON FARMS

In our study, we placed fresh carrion in the stink stations twice, once at their initial deployment and again after 21 days. This was based upon estimating that at an average temperature in Darwin of ~25°, most *Chrysomya spp*. blow flies would complete their lifecycle in ~12 days (Byrd & Butler 1997; Zhang et al. 2019) with an additional 5-7 days before the onset of egg laying (Gabre et al. 2005; Hadura et al. 2018). We hypothesised that adding fresh carrion again after three weeks would help to maintain blow fly populations on farms by providing newly emerged adults with fresh oviposition sites. Two weeks after adding the carrion to the stink stations, we set four commercial fly traps on all the farms to quantify the effects of carrion on fly abundance. The abundance of blow flies trapped on farms with stink stations was consistently higher than on control farms throughout the study, indicating that an interval of three weeks was sufficient to promote the abundance of blow flies.

We also found that the abundance of flies was significantly lower during the second round of trapping compared to the first. This effect occurred regardless of the presence of stink stations, indicating the role of external factors. During the second period of trapping, mango flowering was beginning to decline. Mass flowering crops like mango can be highly attractive to pollinators, temporarily concentrating them within the landscape during the blooming period (Hanley et al. 2011; Holzschuh et al. 2011, 2016; Stanley & Stout 2014). This effect may be even more pronounced in Northern Australia in June and July, when few other plants are flowering (JF, personal observation). We believe that flies may have dispersed away from mango orchards during late flowering, which is why traps on all the farms collected fewer flies. Alternatively, it may be that the commercial fly traps were so effective that using them depleted local populations, resulting in fewer flies being collected during the second trapping period. However, we feel that this is unlikely given the small number of traps used and short trapping periods.

As well as increasing the number of flies trapped on farms, the stink stations also increased the number of flies visiting mango panicles. The effect of the stink stations on blow fly visitation decreased rapidly with increasing distance from the stations (Fig. 4). However, even at distances of up to 30-50 m away from the stations the number of blow flies visiting panicles was still significantly higher than on control farms. How far flies disperse in the landscape is not well understood. Given that flies are highly mobile, are not "central place foragers" and are capable on long distance, migratory movements (Hughes & Nicholas 1974; Wotton et al. 2019; Finch & Cook 2020), dispersal distances are likely to be significant. As such, it is possible that fly abundance was increased far beyond the maximum distance of 30-50 m from stink stations that we tested in our study.

In our study, we observed panicles on trees at increasing distances from stink stations within orchard rows. As such, we do not know how the abundance of flies changed with increasing distance from the stink stations in the adjacent rows. Some orchard pollinators, like honey bees, are known to forage by moving primarily along rows of trees (Kobayashi et al. 2010; Mateos-Fierro 2020) and make infrequent movements between rows. In contrast, non-bee pollinators are believed to make more frequent movements between rows. As such, it may be that the increased abundance of flies around stink stations also occurs in adjacent rows.

THE FUTURE OF STINK STATIONS

We saw no effect of stink stations on fruit set. This may have occurred because of the very high abundance of other native pollinator during our study. Further tests are needed to determine if they could be of use to growers in certain situations, such as where native or managed pollinators are absent or temperatures throughout the flowering are low or unfavourable for other pollinators.

If stink stations were found to be effective under certain conditions, other parameters will need to be further explored to maximise their effectiveness. Our deployment of carrion at three weekly intervals was sufficient to promote blow fly abundance. However, it is possible that earlier, larger, and more frequent additions of carrion may have further increased their numbers during flowering. Further testing is also required to determine the maximum distance at which stink stations promote blow fly abundance both within and between rows. This information will be important for growers in determining the optimum placement of stink stations for their orchards. This distance is likely to be related to the number of flies visiting each station, and thereby, the population density of flies in the local landscape. However, simply adding more stations to farms may dilute blow fly numbers to the point that they are no longer cost effective. In these situations, successive additions of carrion prior to the start of flowering could be used to build blow fly populations to sufficient levels prior to flowering. Local mean temperatures could be used to predict the development time of maggots (Byrd & Butler 1997; Gabre et al. 2005; Hadura et al. 2018; Zhang et al. 2019), ensuring that carrion is provided at the most appropriate time intervals to build their populations.

Any strategies that seek to promote blow fly population densities in the local landscape must also be carefully designed to complement other aspects of farm management, following an integrated pest and pollination approach (IPPM) (Biddinger & Rajotte 2015; Lundin et al. 2021). For example, many growers utilise insecticide sprays during flowering to control pests that attack crop flowers and young fruit. Such sprays are typically performed at night to avoid impacting on managed pollinators but both adult flies, pupae and maggots are likely to be present in the orchards at this time (Sontigun et al. 2018). The use of insecticides is likely to severely impact blow fly populations. Indeed, we believe the application of a dimethoate insecticide during the late afternoon is the primary reason why the stink stations failed on farm PT. Methods must be developed to make the use of stink stations more compatible with other aspects of farm management (Isaacs et al. 2017; Egan et al. 2020; Lundin et al. 2021). For example, the stink stations could be moved away from the crop prior to spraying and returned after pesticide residues have dissipated. This may help to reduce negative impacts on blow fly populations.

One possible alternative to the use of stink stations is to mass rear blow flies using purpose-built facilities and release them into orchards during flowering (Cook et al. 2020). This would have the advantage of giving greater control to the growers in the timing and release of the blow flies, while minimising the negative impacts of predation, parasitism and competition on fly larvae (Grassberger & Frank 2004; Paula et al. 2016; Macinnis & Higley 2020). However, such mass releases could have broader social or ecological consequences. For example, mass released flies could become a nuisance for nearby residents if large numbers of flies enter homes. Importing and releasing blow flies from other regions may also negatively impact on ecosystems around the release site through competition with local species or locally adapted genotypes of the same species. Care must be taken to avoid unintended effects on the local community and ecosystems (David et al. 2013).

CONCLUSIONS

This study is an important test of the stink station concept. The methods used here successfully increased the abundance of blow flies in mango orchards and this increase was significant at distances of at least 30-50 m. Although we did not detect an observable increase in fruit set because of increased blow fly activity, we believe that such increases may only occur under particular conditions, such as where the number of other pollinators is low, perhaps as the result of environmental factors (i.e. drought, bush fires). Further research is required to determine if stink stations are a viable option for growers where wild or managed pollinator populations are reduced. In further researching the use of stink stations, we hope to provide growers with robust and cost-effective alternatives to the use of conventional managed pollinators, as well as promoting the use of diverse assemblages of wild pollinators in agriculture.

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AUTHOR CONTRIBUTION

JF acquired the funding, designed the study, collected the data, analysed the results and wrote the manuscript. AMG designed the study and wrote the manuscript. JC acquired the funding designed the study and wrote the manuscript. All authors read and approved the final manuscript.

DATA AVAILABILITY

The datasets supporting the conclusions of this article have been made publicly and permanently available in the Figshare online repository https://doi.org/10.6084/m9.figshare.21804414.

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