Calibration and Validation of Honey Bee (*Apis mellifera*, L.) Flight Duration as a Predictor of Distance Flown

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ABSTRACT

Organic beekeeping standards require that beekeepers provide for their honey bees (*Apis mellifera*, L.) with a radius of 6.4 km of foraging land that is free from (3 km) or with reduced use of (additional 3.4 km) synthetic pesticides. This requirement is based on the honey bee's large maximum foraging range of 10-12 km, even though most foraging trips occur at c. 2 km from the hive. Because of this mismatch between organic foraging range requirements and more recent foraging range data, large scale honey bee foraging patterns on organic farms need to be investigated. But, current methods of estimating honey bee foraging ranges, including our current gold-standard of waggle dance decoding, are unsuitable for use in a large-scale, organic farm context. One potential new method of estimating distance flown is by using a bee's flight duration, or the time she spends outside the hive. However, what is not known is how, or how well, durations translate to distance. Here, we test the viability of the new method first with a Calibration Experiment, where we observed the flight durations of individually marked bees foraging at known distances. Then we performed a Validation Experiment, where we used a model fitted to the Calibration Experiment's data to predict flight distance from flight duration for freely flying bees, which we then compare to a distance estimate generated from the same bee's decoded waggle dance. We found in our Calibration Experiment that flight duration had a significant, positive relationship with distance flown when bees foraged upon artificial feeders. We then created two Calibration Models that both produced accurate, but imprecise, predictions of distance for bees traveling to feeders. These predictions were significantly correlated with the true, measured distances, as tested both with our analysis bees and a hold-out sample, which were not part of the main analysis (analysis population: $p < 0.001$; holdout sample: $p < 0.001$). However, the Validation Experiment revealed that a freely foraging bee's flight duration is not significantly related to her waggle run duration which has a known, linear relationship with distance. Therefore, flight duration did not produce accurate estimates of distance flown for freely foraging bees that, importantly,

recruited nestmates. This may be because the use of dancing (recruiting) bees nonrandomized the sample of foragers. Additionally, we observed that pollen foragers had significantly longer flight durations (24.5 ± 11.8 minutes) than nectar foragers (16.7 ± 8.8 minutes; $p < 0.001$), even though pollen foragers had significantly shorter waggle run durations (1.11 ± 0.5 s) compared to nectar foragers (1.60 ± 0.42 s; $p < 0.001$). Overall, these results reveal that we can use flight duration as a proxy for distance, but cautiously, as predictions will be noisy and often reflect the upper boundary of flight distance for a given duration. Although we cannot yet explain why the validation does not support our calibration, we suspect that the sub-selection from freely foraging bees to those that are also at the stage of making a recruitment dance, interacting with different dance thresholds for differing resources, may produce the observed inverse relationship. Future work should track the flight duration ontogeny of bees foraging at known distances until they produce a waggle dance, which will allow us to determine the potential impact of distance, resource reliability, and optimized flight durations on waggle dance production.

Calibration and Validation of Honey Bee (*Apis mellifera*, L.) Flight Duration as a Predictor of Distance Flown

Lindsay Johnson

GENERAL AUDIENCE ABSTRACT

Honey bees (*Apis mellifera*, L.), important pollinators that can be managed through beekeeping, can be exposed to pesticides that cause adverse effects while foraging on flowers. Organic beekeeping, an alternative method of beekeeping that seeks to reduce artificial chemicals in honey and other products, requires that beekeepers provide a large amount (6.4 km radius) of land for foraging that either has no or very little synthetic pesticides because honey bees have a large maximum flight distance (10-12 km from their hive). However, it may be that most flights are at shorter distances. We need more and better information on how far bees are actually flying to forage. Unfortunately, many current methods, including our gold standard that uses the honey bee's recruitment communication called the waggle dance, are unsuitable for big, field-based projects. Could flight duration, or how long a foraging bee is outside the hive, be used to estimate flight (or forage) distance? Here we performed two experiments to answer this question. In a Calibration Experiment, we measured individual bee flight durations as they visited an artificial feeder, which was placed at known distances. In a Validation Experiment, we compared flight durations of bees that foraged naturally in the landscape to the distance the bee communicates with her waggle dance. We found that, when bees foraged on feeders, their flight durations increased when the distance they flew increased. Given that result, we were able to make predictions of distance flown from flight durations. Additionally, it may be that these predictions provide a maximum distance estimate for a given duration. However, we were unable to validate the predictions because when bees fed on flowers, we observed that their flight durations slightly decreased when their waggle dances indicated a further distance. Therefore, our calibration does not produce a good distance estimate when applied to bees that also performed waggle dances. We also found that pollen foraging bees took a longer amount of time to forage than nectar foraging bees, despite the fact that our pollen foragers visited flowers at a shorter distance than the nectar foragers, as estimated from their waggle dances. Overall, our calibration may be used to

predict a maximum flight distance for a given duration, but that these predictions will be inexact. Future work should untangle the potential interactions of recruitment, whether the bee is foraging for pollen or nectar, and foraging distance on the flight durations of bees.

Dedicated to Reba, Dolly, Patsy, and James, the queens whose daughters were the subjects of my research.

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Introduction

75% of the leading global crop species are dependent upon or benefit from animal pollination and, due to the growing human population, the fraction of crops that require pollination by animals has increased by 300% in the past 50 years (Klein et al. 2006; Garibaldi et al. 2009; Aizen and Harder 2009). Of the animal pollinators, bees provide approximately 62% of pollination visits to crop flowers (Rader et al. 2016), and within the bees, honey bees are economically important and provide the majority of services to several crops, including almonds and blueberries (Reilly et al. 2020). In the United States alone, honey bee pollination services are valued at $17 billion annually, with an additional $370 million valuation for honey production (Woteki 2013; National Agricultural Statistics Service 2023). Despite the need for these bees, the number of managed colonies in the United States has declined by 61% over the past 70 years, even while the number of managed colonies has increased worldwide (Aizen and Harder 2009; vanEngelsdorp and Meixner 2010; Wagner et al. 2021). In sum, the supply of these pollinators is insufficient to keep pace with the increased demand for their services (Aizen et al. 2008; Aizen and Harder 2009).

These declines are due to several factors that singly, and in combination with one another, detrimentally impact individual bee and colony-level health and survivorship (vanEngelsdorp and Meixner 2010; Vanbergen 2013; Goulson et al. 2015; Grab et al. 2019; Ramos-Jiliberto et al. 2020). Firstly, honey bees are susceptible to a variety of pathogens, including Deformed Wing Virus (DWV) and *Variforma* (Martín-Hernández et al. 2007; Gisder et al. 2009; Goulson et al. 2015). Honey bees also contend with hive pests and parasites, most notably the mite, *Varroa destructor*, which vectors DWV. Third, agricultural intensification and urbanization has greatly reduced the amount and diversity of floral resources, such that bees must forage on a more monotonous and nutritionally depleted landscape (Pywell et al. 2005; Donkersley et al. 2017). Because honey bees are generalist pollinators that benefit from a varied diet, a lack of floral diversity can result in a weakened colony that is more susceptible to pests and diseases (Alaux et al. 2010b).

Finally, while pesticides are necessary to produce crops at the scale on which we need them, they can adversely affect the health of honey bees (Wu et al. 2012; Goulson et al. 2015; Thorbek et al. 2017; McHenry et al. 2025a). Even if pesticides do not cause lethal events, the sublethal effects of many agrochemicals may be deadly in combination with other stressors (Henry et al. 2012; Smith et al. 2013). Bees raised in high-pesticide residue comb were more susceptible to *Nosema* and were symptomatic at younger ages compared to bees reared in low-pesticide residue comb (Wu et al. 2012). Neonicotinoid exposure, even at low levels, can cause immunosuppression, promote the replication of DWV, and increase mortality due to *Nosema* infections (Alaux et al. 2010a; Di Prisco et al. 2013; Goulson et al. 2015). In addition, neonicotinoids impair olfactory learning, interfere with navigation, and decrease foraging activities, all of which could lead to lower hive productivity (Decourtye et al. 2004; Henry et al. 2012; Fischer et al. 2014; Ohlinger et al. 2022a). Glyphosate, an herbicide, can perturb the gut microbiome of honey bees, which could lead to an increased risk for disease (Goulson et al. 2015; Motta et al. 2018, 2022). Recently, glyphosate was also found to negatively impact foraging frequency and to alter biogenic amines present in the honey bee mushroom body (McHenry et al. 2025a). Because of these damaging effects of pesticides on honey bees, their use must be carefully traded off against the health of insect pollinators, including managed honey bees. One potential way to reduce pesticide exposure to bees is by adopting alternative management practices, like organic beekeeping that limit the use and presence of synthetic chemicals. While organic beekeeping is promising, and confers many benefits, it is difficult for beekeepers to obtain organic certification, thus limiting market potential.

Flight duration is predictive of distance flown for bees foraging on artificial feeders, but not for freely foraging, waggle-dancing bees

Abstract

Organic beekeeping standards require that beekeepers provide for their honey bees (*Apis mellifera*, L.) with a radius of 6.4 km of foraging land that is free from (3 km) or with reduced use of (additional 3.4 km) synthetic pesticides. This requirement is based on the honey bee's large maximum foraging range of 10-12 km, even though most foraging trips occur at c. 2 km from the hive. Because of this mismatch between organic foraging range requirements and more recent foraging range data, large scale honey bee foraging patterns on organic farms need to be investigated. But, current methods of estimating honey bee foraging ranges, including our current gold-standard of waggle dance decoding, are unsuitable for use in a large-scale, organic farm context. One potential new method of estimating distance flown is by using a bee's flight duration, or the time she spends outside the hive. However, what is not known is how, or how well, durations translate to distance. Here, we test the viability of the new method first with a Calibration Experiment, where we observed the flight durations of individually marked bees foraging at known distances. Then we performed a Validation Experiment, where we used a model fitted to the Calibration Experiment's data to predict flight distance from flight duration for freely flying bees, which we then compare to a distance estimate generated from the same bee's decoded waggle dance. We found in our Calibration Experiment that flight duration had a significant, positive relationship with distance flown when bees foraged upon artificial feeders. We then created two Calibration Models that both produced accurate, but imprecise, predictions of distance for bees traveling to feeders. These predictions were significantly correlated with the true, measured distances, as tested both with our analysis bees and a hold-out sample, which were not part of the main analysis (analysis population: $p < 0.001$; holdout sample: $p < 0.001$). However, the Validation Experiment revealed that a freely foraging bee's flight duration is not significantly related to her waggle run duration which has a known, linear relationship with distance. Therefore, flight duration did not produce accurate estimates of distance flown for freely foraging bees that, importantly, recruited nestmates. This may be because the use of dancing (recruiting) bees nonrandomized the sample of foragers. Additionally, we observed that pollen foragers had significantly longer flight durations (24.5 ± 11.8 minutes) than nectar foragers (16.7 ± 8.8 minutes;

$p < 0.001$), even though pollen foragers had significantly shorter waggle run durations (1.11 ± 0.5 s) compared to nectar foragers (1.60 ± 0.42 s; $p < 0.001$). Overall, these results reveal that we can use flight duration as a proxy for distance, but cautiously, as predictions will be noisy and often reflect the upper boundary of flight distance for a given duration. Although we cannot yet explain why the validation does not support our calibration, we suspect that the sub-selection from freely foraging bees to those that are also at the stage of making a recruitment dance, interacting with different dance thresholds for differing resources, may produce the observed inverse relationship. Future work should track the flight duration ontogeny of bees foraging at known distances until they produce a waggle dance, which will allow us to determine the potential impact of distance, resource reliability, and optimized flight durations on waggle dance production.

Introduction

Organic beekeeping, a management style that aims to reduce synthetic pesticide levels in honey bees and in the products made by them, confers benefits both to the bees and the beekeepers who maintain them. Across a three-year study, organically managed colonies had increased honey production, increased profitability, cleaner hive products, and similar survivorship when compared to conventionally managed colonies (Underwood et al. 2023, 2025). However, although 24% of U.S. beekeepers avoid the use of synthetic pesticides, they are unable to market their products as organic as they cannot meet current United States Department of Agriculture (USDA) guidelines for organic beekeeping (Giacomini 2010; Underwood et al. 2019). Organic beekeepers must provide a 3 km forage zone around the bees that is free of synthetic pesticides and other chemicals, as well as an additional 3.4 km surveillance zone with minimal synthetic contamination to be eligible for certification (Giacomini 2010). This vast foraging arena totaling 6.4 km is impractical for beekeepers in the continental U.S. to provide for their bees, and only beekeepers in Hawai'i are able to meet this standard ("Organic Integrity Database").

These stringent recommendations are based on the honey bee's ability to forage, under certain conditions, at 10-12 km (von Frisch 1967; Beekman and Ratnieks 2000). Indeed, while honey bees can reach these extreme distances, the majority of foraging trips usually occur much closer to the hive, between 1-2 km, with long distance foraging comprising only 1-2% of all advertised trips across the entire foraging season (Steffan-Dewenter and Kuhn 2003; Greenleaf et al. 2007; Couvillon et al. 2014b, a, 2015b; Danner et al. 2016; Silliman et al. 2022; Steele et al. 2022; Ohlinger et al. 2022b).Therefore, there is a mismatch between the range requirements for organic certification and recent data on the advertised distances at which freely flying honey bees typically forage, making the relevance of the requirements unclear. What is needed is better and more data on honey bee foraging distance, in particular on organic farms where floral resources may be in abundance, making long distance foraging unnecessary.

Our current gold-standard for estimating flight distance is by decoding waggle dances, a communication behavior honey bees use to inform nestmates of optimal foraging locations (von Frisch 1967; Seeley 1995; Couvillon 2012). This dance consists of two phases: the return phase and the waggle run, which is the information-rich portion of the dance (Seeley et al. 2000). The dancing bee expresses distance traveled by the duration of the waggle run and the direction of her flight as the angle of her dance relative to the vertical (von Frisch 1967; Seeley 1995). These dances can be decoded by human observers to create estimates of where the dancing bees foraged, including the approximate distance of their flights (Couvillon et al. 2012, 2014b, a; Schürch et al. 2019; Steele et al. 2022; Ohlinger et al. 2022b, 2024).

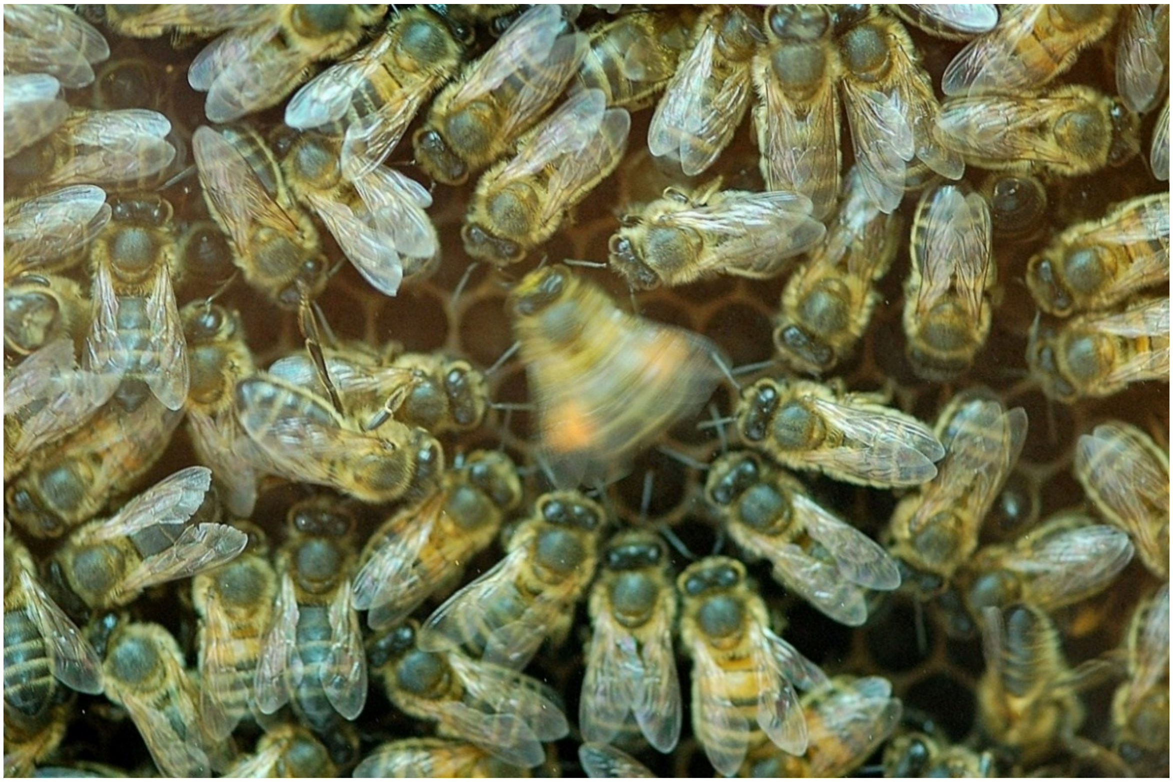

Figure 1: A successful pollen forager performs a waggle dance. Photo by Christoph Grüter.

While this method is widely used in both fundamental and applied studies of honey bee foraging, it is not without its limitations. Firstly, because waggle dances only communicate the location of sites with the most profitable forage, their use in honey bee foraging investigations means that data do not depict the entirety of honey bee foraging options, but rather the best ones currently being exploited by the hive. This filtering means that dancers are, by definition, a nonrandom selection of overall foragers, which may have bearing in studies looking at the entirety of forager populations. Next, to observe and decode dances, the bees must be housed in glass-walled observation hives, which are smaller than typical Langstroth hives, and they must be kept indoors (Seeley 1995). Therefore, these hives cannot be placed in the field. Additionally, decoding dances is an extremely time and labor-intensive process because dances have to be decoded one at a time and by hand and there is not yet a way to automate dance decoding in a reliable, sensitive manner (Couvillon et al. 2012; Couvillon and Ratnieks 2015; Wario et al. 2015; Okubo et al. 2019). As such, dance decoding is not suitable for any studies that involve large numbers of freely flying individuals from full-strength, regular hives, which would be essential in a large-scale investigation of foraging distances, including on organic farms.

One potential method that may provide the critically needed data involves the use of a hive entrance detection system to identify individually marked bees as they enter or exit the hive (Chen et al. 2012; Campbell et al. 2023; Penaloza-Aponte et al. 2024; Brandt et al. 2025). Such a system may be modified to record automatically the flight durations (amount of time between a bee exiting the hive and returning to it) of individual bees, and it was hypothesized that these durations may then be used to estimate flight distances for many bees in the field (Penaloza-Aponte et al. 2024; Brandt et al. 2025). However, what is not known is how these durations translate into distance, and whether this translation works well across different distances.

Here we tested the rigor of flight duration estimates as predictors of flight distance in two field experiments, a calibration and a validation. First, we created a flight duration-to-distance calibration by training individually marked bees to forage at different, known distances, which we analyzed against their individual flight durations for that given distance. Second, we performed a Validation Experiment, where we allowed individually marked bees to forage freely at unknown locations in the landscape and collected both flight duration and waggle dance data from the same bee. These data were then used to generate two distance estimates, one from our calibration using the duration and one from the bee's waggle dance, which she performed upon her return to the hive. We then compared the two distance estimates as a potential validation for our created calibration.

Materials and Methods

Study Organism and Trial Details

We studied four queenright honey bee colonies (A-D, with A-C for both Calibration and Validation and Hive D for Validation only) of mixed lineage, each with brood and ca. 3000-5000 workers. Each colony was housed in a glass-walled observation hive in our field laboratory at Prices Fork Research Center in Blacksburg, VA, about four miles from the main campus of Virginia Tech. All the hives were composed of three full depth frames and connected to the outdoors via a 3x30 cm PVC tube. On non-experimental days, we provided supplemental feeding to the bees with a 1M sucrose solution. For the Calibration experiment, we collected field data across three trials from 12 June – 11 July 2024, working sequentially with one colony per trial. Once a colony completed its Calibration Experiment, we allowed for worker turnover and then used it for the Validation Experiment. For the Validation Experiment, we collected field data across two trials in the summer and early fall (Colonies B and C 22 July – 11 September 2024), with a third trial in the following spring (Colony D, May 2025). We did perform a validation trial with Colony A in Spring 2024 but were unable to use the data because of technical difficulties with the detection system that ultimately led to our adoption of number tags instead of AprilTags to mark the bees (see below).

Measuring Flight Duration with a Hive Entrance Detection System

It was necessary for us to measure flight duration of individual bees for both calibration and validation. To do this, we employed a hive entrance detection system (Figure 2) that consisted of a Raspberry Pi computer (Figure 2A) with a camera attachment (Figure 2B), housed in a junction box and affixed atop the hive entrance (Penaloza-Aponte et al. 2024). Because our study colonies were housed in observation, not Langstroth, hives and must access the outdoors via a pipe that went through the wall, we 3D-printed a custom platform that would optimize the camera's view of the bees and support the computer's weight on the tube (Figure 2C). We used a wooden platform on an adjustable tripod to provide further support in the event of windy weather.

Because our experimental methodology (see below) required that we easily and quickly identify the bees in real time as they visited the feeder (calibration) or danced (validation), we individually marked our bees with numbered queen-marking tags (Queen Number Set, Betterbee, Greenwich, NY), which meant that we could not use the detection system in its fully automated form that is optimized to read AprilTags (Penaloza-Aponte et al. 2024; Brandt et al. 2025). Rather, we filmed the entrance platform with the camera attachment during both our calibration and validation trials and then viewed the footage to record the identity and timestamp of marked bees as they either entered or exited the hive, which we then used to calculate flight duration for the given experiment.

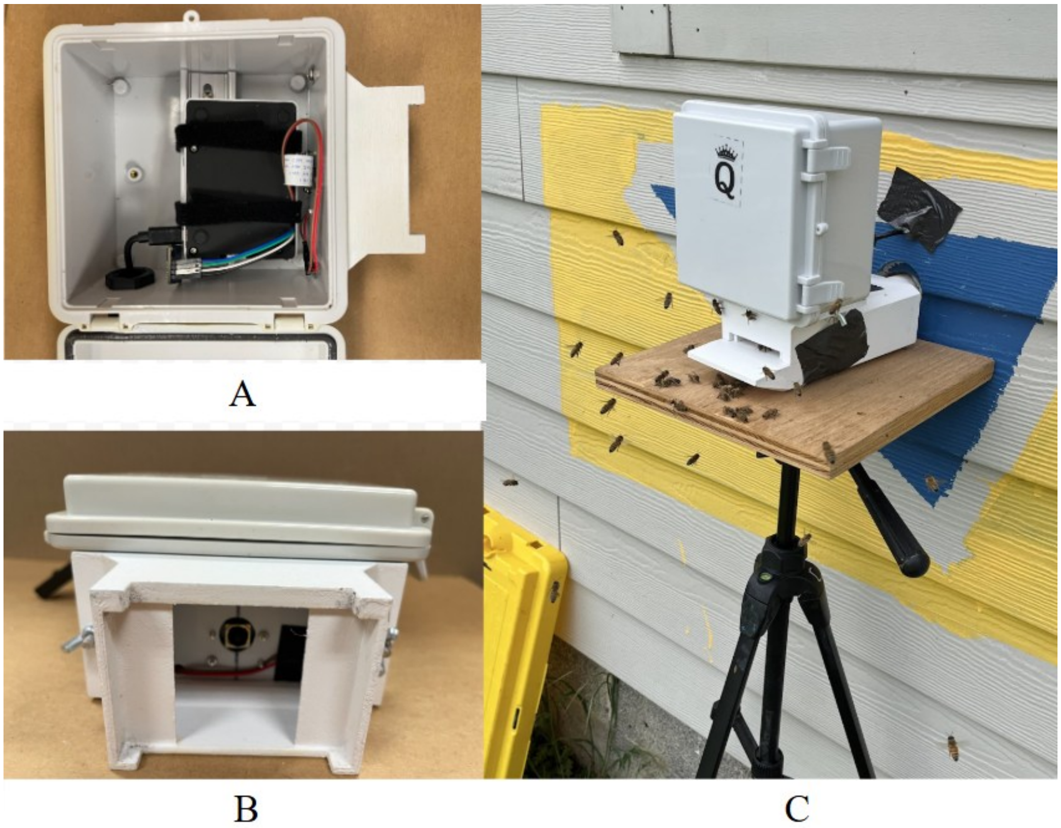

Figure 2: We used a hive entrance detection system, adapted from Peñaloza-Aponte et al. (2024), in both our calibration and Validation Experiments A) the Raspberry Pi rests inside its protective junction box. B) a view of the camera inside its enclosure that filmed the entrance and exit of all bees, including our marked, experimental bees. C) the entire detection system affixed to the observation hive entrance.

Experimental Methodology: Calibration

The goal of our Calibration experiment was to analyze bee forager trip duration against distance. This goal required that we train individually marked honey bees to collect sucrose solution from a feeder placed at different, known distances. These highly committed foragers then make multiple foraging trips to each feeder, and their individual identification meant we could collect verified trip duration data (i.e., we can align an individual's trip duration with an identified feeder visit).

To accomplish this goal, we trained worker bees to forage at an artificial feeder filled with a 2M sucrose solution and scented with either 10 uL/L lavender (Trial 1) or 10 uL/L linalool (Trials 2-3). Ultimately, we recorded feeder visits and flight durations for 6-7 distances, between 36 m and 611 m (Figure 3). We chose to work in high summer because honey bees are more motivated to visit artificial feeders in times of relative forage dearth (Couvillon et al. 2014b, 2023, 2024; Balfour et al. 2018; Ohlinger et al. 2022b).

For our feeder training, we used a modified version of the method employed in Schürch et al., (2019). Briefly, we began each trial with a pre-training phase where we encouraged an initial cohort of bees to visit a Petri dish filled with a 2M scented sucrose solution by placing the dish on a tripod platform immediately outside the observation hive tube, which made it easy for foragers to discover it as they exited the hive. When a bee from our target observation hive started to drink, we glued the individual number tags on their thorax before returning them to the Petri dish, where they usually continued to drink. Because of the presence of a nearby apiary, we carefully monitored any bees that we tagged to confirm that they went back inside the tube of our observation hive. Recruitment from a full-strength colony from the apiary can quickly overwhelm our experiment, so it was important during our trials to ensure that we were only ever working with bees from our experimental observation colony.

After c. 10 marked bees accumulated on the dish, we moved it to another adjacent platform, covered in a blue plastic tablecloth, and swapped the Petri Dish for a feeder, consisting of a 4 oz glass jar (approximately 29.6 ml; Ball, Westminster, CO, USA) inverted over a plastic base with several scored troughs, filled with the same 2M sucrose solution. Then we began to step the feeder further away from the hive, a few meters at a time, allowing the bees to find and to drink from the feeder at each step. Then, once we were a few meters shy of the first Experimental Location, we allowed the bees to visit the feeder for approximately 30 minutes before removing the feeder and tripod with the approach of evening, thus concluding our pre-training phase.

We began the training phase on the following morning (Experimental Day 1) by setting up the feeder station, consisting of the same tripod and plastic tablecloth, in the same location as the end of the previous day, and with the same sucrose solution as the day before. Once the bees began to visit the feeder consistently, which usually occurred within a few minutes of returning the setup to the field, we performed one more step, which moved the feeder to the first Experimental Location (approx. 46 m from the hive, as measured with Google Maps 'measure distance' tool; Figure 3). Concurrently, we turned on the camera on our hive entrance detection system to record entrance/exits of marked bees. Then we began to record the identity and time of every marked forager that drank from the feeder in ODK data collection sheets. We continued collecting these data for about an hour, which allowed each marked, experimental bee the opportunity to make multiple, independent foraging trips. After the hour, we stopped the camera and began once again, in stepwise fashion, to move to the second Experimental Location at approx. 147 m from the hive (Figure 3). We always moved the feeder a few meters at a time, stopping at each intermediate location for at least 10 minutes to allow bees to find us and to drink from the feeder. Once we arrived at the next Location and each of the tagged experimental bees found the feeder, we once again began recording hive entrance video and collecting feeder data. Then we repeated these steps for the third Experimental Location. We usually were able to obtain data for three or four Locations on Experimental Day 1 of each trial.

On Experimental Day 2, we returned to the last feeder location from the previous day and waited for the bees to rediscover the feeder before we began moving toward the next experimental location. We repeated our steps until we had completed the remaining three Experimental Locations (Figure 3). At the end of the trial, we removed all the feeders from the field, fed the colony in the observation hive, and then left it undisturbed for a few weeks until it was time for the Validation Experiment (see below).

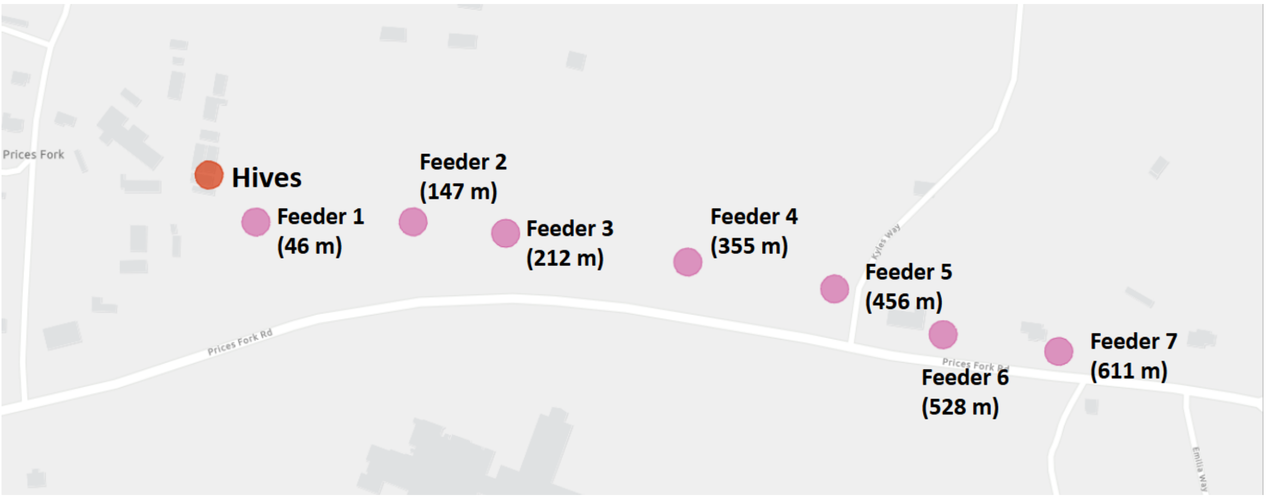

Figure 3: The location of the hives (A-C), shown in red, and feeder locations, shown in magenta, on a map. Bees in Trials 1 and 3 were trained up to Feeder 6 (528 m) and bees in Trial 2 were trained to Feeder 7 (611 m).

Measuring Crop Fill Time

Honey bees occasionally leave their colony briefly for non-foraging needs, such as evacuation flights (Winston 1991). To eliminate a majority of these non-foraging trips from our dataset of flight durations, we determined the average time that it took for a honey bee to fill her crop from our artificial feeders. We reasoned that since our calibration bees engaged in crop filling in addition to flying back and forth to the Experimental Locations, if a bee presents with a flight duration less than the average crop fill time, it would be highly unlikely that she foraged (i.e., flew and drank) from the feeders. Four such trips were excluded from our dataset. For this measurement, we set out an artificial feeder, identical to the ones we used in our calibration trials, at the apiary adjacent to our bee field lab in Blacksburg, VA. Then, we monitored and recorded the duration of freely flying bees that visited the feeder and drank. We collected these data twice (20 September 2024, n = 100 feeder visits) and 22-23 May 2025, n = 37 feeder visits).

Experimental Methodology: Validation

The goal of our Validation experiment was to collect both waggle dance data and trip duration data from the same individually marked bee. The latter would be used to estimate flight distance using our newly created Calibration (see above). The former would be used to validate the distance estimate obtained from the calibration: in the waggle dance, a bee communicates the distance and direction from the hive to the forage, which we can decode and convert to location, including a foraging distance (Schürch et al. 2013, 2019). We used distance estimates made with decoded waggle dances as a point of comparison due to it's widespread use and accuracy (von Frisch 1967; Couvillon 2012; Couvillon et al. 2014b; Ohlinger et al. 2022b; Ostrom et al. 2025).

To accomplish this goal, it was important that forager bees already possess an individually identifying tag before the onset of the Validation experimental trials, which we did in two ways. For Trial 1, we placed a frame of capped, pupating, brood in an incubator set to 34-35 C. The frame was from the same colony that also was in our observation hive as part of the Calibration experiment. For a week, we would collect newly emerged bees and mark them daily with the same individual number tags and shellac as the Calibration experiment. At the end of each marking day, we placed the newly tagged bees in a jar with a mesh lid, which was then inverted over a round mesh hole in the top of the observation hive that is typically used for supplementary sucrose feedings. This allowed the colony to become accustomed to the odors of the bundle of newly marked, newly emerged bees while keeping them physically separate. Then, 8-12 hours later, we slowly introduced the new bees to the hive through an opened ventilation hole in the hive while also providing a rewarding sucrose solution with a quick syringe squirt through the same hole. The combination of the newcomers being in proximity for hours before introduction and the sucrose solution peace-offering allowed for a high proportion of acceptance for the new nestmates. Following these successful introductions, we waited to start the Validation Trial until we noticed the first of our marked bees foraging and dancing (approx. 3 weeks following emergence/marking).

In Validation Trials 2-3, we noticed that our introduction protocol was no longer working, as we observed that the introduced bees were immediately and viciously attacked inside the observation hive. Therefore, we switched to capturing adult, flying bees at the hive entrance using queen cages and marking them with number tags, even though this resulted in our being able to mark fewer overall number of bees. The marked bees would then be allowed to fly and to enter the entrance tube on their own. Because the marking was then done on older bees that were already flying, we were able to start our Validation trial on the next day.

As in the Calibration experiment, we filmed the hive entrance during trial periods so that we could later identify individual flight durations (see below) of our experimental bees. Concurrently, we also filmed inside the observation hive to record the waggle dances performed by the marked bees from whom we also collected trip durations. We filmed the observation hives using a Canon HF G50 Video Camera for 1-3 hours each day. Following these trials, we identified individual dances in the videos and took note of the identity of the bee that performed them and when they occurred. We then analyzed the hive entrance video for entrance and exit events, calculated the flight durations for marked bees, and matched them to the corresponding waggle dances. Not every bee that forages will dance (von Frisch 1967; Seeley 1994; Couvillon et al. 2015a). Therefore, for all bees from whom we were able to calculate trip duration, we would expect a small subset of them to also perform a waggle dance. We ultimately found a total of 172 flight duration and waggle dance pairs – 16 from Trial 1, 1 from Trial 2, and 155 from Trial 3. This difference in numbers between trials was due to us only filming the bees for a period of c. 1 hour for Trials 1 and 2, in contrast to c. 2-3 hours in Trial 3. Prior to completing Trial 2 and beginning our video analysis, we were unaware how long honey bee flight durations could be, oftentimes in excess of 30 minutes. That is why we adjusted our filming duration for Trial 3.

To obtain a distance estimate from waggle dances, we first converted waggle dance video files from MP4 to AVI format using ffmpeg v 7.1.2. We then imported each file into ImageJ v. 1.54r and decoded using a modified format of the methods described in Couvillon et al. (2012). For this project, we were only interested in the distance component of the dance, which is encoded in the duration of the waggle run (von Frisch 1967; Couvillon et al. 2012; Schürch et al. 2013, 2019). We determined a bee's waggle run duration as the difference between the start frame and the end frame of each run, with each second of duration being ca. 645 m of distance (Schürch et al., 2019). For each dance, we decoded a subset of four, non-first, non-last waggle runs, which was shown to provide a representative and consistent sample of the information in the whole dance (Couvillon et al. 2012).

Finally, we noted whether the dancing bee had visible pollen in her corbiculae. Because water foragers can comprise less than 1-5% of non-pollen foragers (Couvillon et al. 2014b), we labeled all non-pollen foragers as nectar foragers.

Data Analysis: Calibration

All analyses were performed in R v.4.3.0. We used the function distHaversine() from the package geosphere v.1.5-20 to calculate the distances between the hives and feeder locations based on the coordinates collected in the ODK sheets (Hijmans et al. 2024). Then, using our average crop fill time, we cleaned our dataset of any flight durations that were too short to allow for flight and drinking from feeders. We ultimately analyzed 1390 feeder visits and flight duration pairs (260 from Trial 1, 878 from Trial 2, and 252 from Trial 3) from 57 bees (12 from Trial 1, 26 from Trial 2, 19 from Trial 3).

To internally validate the flight duration-distance calibration, we randomly selected 2 bees from each of the three trials (3.7% of the total population of experimental bees) to be a part of a hold-out sample. The remaining experimental Calibration bees (n = 51) and their flight duration-feeder visit pairs comprised our analysis population that we then used to create our Calibration Models, which we could then verify with the hold-out sample.

After determining that the distribution of the flight duration data was positively skewed and therefore limiting for linear modeling, we opted to log-transform it. We used this log-transformed data to determine the relationship between distance and duration using a linear-mixed effect model from the package lme4 v.1.1-37 (Bates et al. 2015, 2025). We generated a list of all possible combinations of distance-duration pairs based upon the data from the Calibration Experiment with the expand.grid() function. Using this list and the Log-Transformed Linear Model (log(flight duration) ~ known distance + (1 | individual bee's ID) + (1 | Hive)), we estimated distances for each flight duration for both our analysis population and our hold-out sample.

Additionally, we also created a 5th Quantile Regression Model (rq(log(flight duration)) ~ known distance, $\tau = 0.5$) using the package quantreg v. 6.1 to generate the farthest possible distance flown for a given flight duration (Koenker et al. 2025). This model did not include any random effects. Using the 5th quantile, allows us to see what the approximate lower bound for the time a bee needs to travel to each of our distances. As with our linear model, we used log-transformed flight durations from our analysis population in the 5th Quantile Regression Model. Again, we made a list of all possible distance-duration pairs using the expand.grid() function and used both this list and our 5th Quantile Regression Model to estimate distances for both our analysis population and hold-out sample.

Finally, we completed our internal validation by performing Kendall's Rank Correlation Test to estimates made from the Calibration model for both the analysis population and hold-out sample. This test evaluates the relationship between two ranked variables, in this case our estimated distances and our known, experimental distances. If the hold-out sample and analysis population possess similar correlation coefficients for the same model, it indicates that the model produced good estimates of distance for the bees visiting the feeder.

Data Analysis: Validation

To estimate distances based on waggle run duration, we used the universal calibration reported in (Schürch et al. 2019). Because there is inter-dance variation among individual bees within a colony and negligible variation between colonies, it should be applicable for any landscape and location to create distance estimates from waggle run durations (Schürch and Couvillon 2013; Schürch et al. 2013, 2016a, 2019). Indeed, the universal calibration has been externally validated and used in numerous studies since its publication (Carr-Markell and Spivak 2021; Samuelson et al. 2022; Steele et al. 2022; Ohlinger et al. 2022b, 2024; Wu et al. 2024; McHenry et al. 2025b; Wang et al. 2025; Ostrom et al. 2025).

Then we used both the Log-Transformed Linear Model and the 5th Quantile Regression Model to estimate distances based on the flight durations of freely foraging bees observed in our Validation experiment. Therefore, for each foraging trip performed by an individually marked, freely flying bee, we possessed three distance estimates - one from the decoded waggle dance duration and two generated from our two Calibration models using flight duration. Then we performed Kendall's Rank Correlation Test on flight duration-distance estimates and waggle run distance estimates for all bees regardless of foraged resource (nectar versus pollen). Lastly, we used linear mixed-effect models and likelihood ratio tests to determine if resource type (pollen or nectar) was a significant predictor of flight duration-distance estimate accuracy.

Results

Honey Bees Drink Quickly on Artificial Nectar Feeders

We recorded 138 crop fill times that ranged from 10.7 - 168.7 seconds, with a median time of 43.5 s and a mean time of 47.1 s (Figure 4). The positively skewed nature of the distribution reflects a few extreme outliers, but those represented c. 2% of the data.

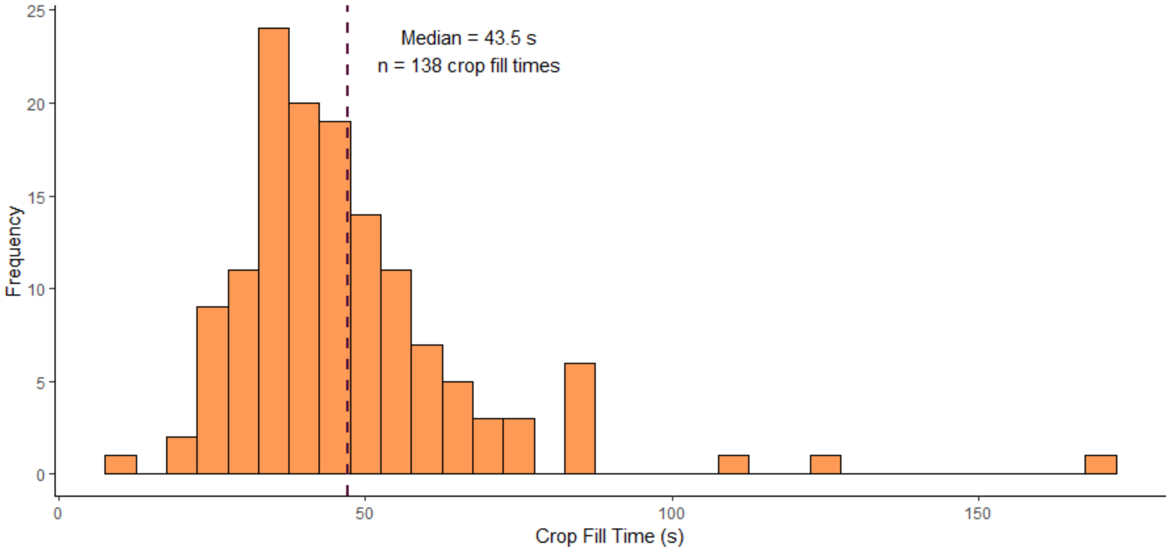

Figure 4: Bees took a median of 43.5 seconds to fill their crops at the feeders. The X axis is the time in seconds it took bees to drink to completion on an artificial feeder. The Y axis is the frequency.

Flight Duration Significantly Increases with Distance for Both the Log Transformed Linear Model and the 5th Quantile Regression Model

With our Log-Transformed Linear Model, we found that flight duration significantly increased with feeder distance, so that for each additional 100 m of distance, the log of flight duration increased by 5.956e-01 (1.8 minutes when back-transformed) (likelihood ratio test (LTR): Chisq = 50.8, Df = 4, $p < 0.001$; Figure 5). When back-transformed to our original scale, at our shortest distance of 46 m, the geometric mean for flight duration was 1.94 (1.92 - 1.97) min. At our longest feeder distance (611 m), the geometric mean of the flight duration was 4.68 (4.61 - 4.75) min.

With our 5th Quantile model, we also found that flight duration significantly increased with feeder distance, so that for each 100 m of distance, the flight duration increased by 0.98 minutes (likelihood ratio test (LTR): Chisq = 1.39, Df = 2, $p < 0.001$; Figure 5). When back-transformed to our original scale, at our shortest distance of 46 m, the geometric mean for the 5th quantile for flight duration was 1.08 (1.06 - 1.10) min. At our longest feeder distance (611 m), the geometric mean of the 5th quantile for flight duration was 3.49 (3.42 - 3.56) min.

Lastly, our mean flight duration across all experimental distances (Figure 6) was 2.94 ± 1.5 minutes, with a median of 2.83 minutes. Both models (Log-Transformed Linear and 5th Quantile

Regression) were then used to generate distance estimates from flight durations for unknown foraging locations.

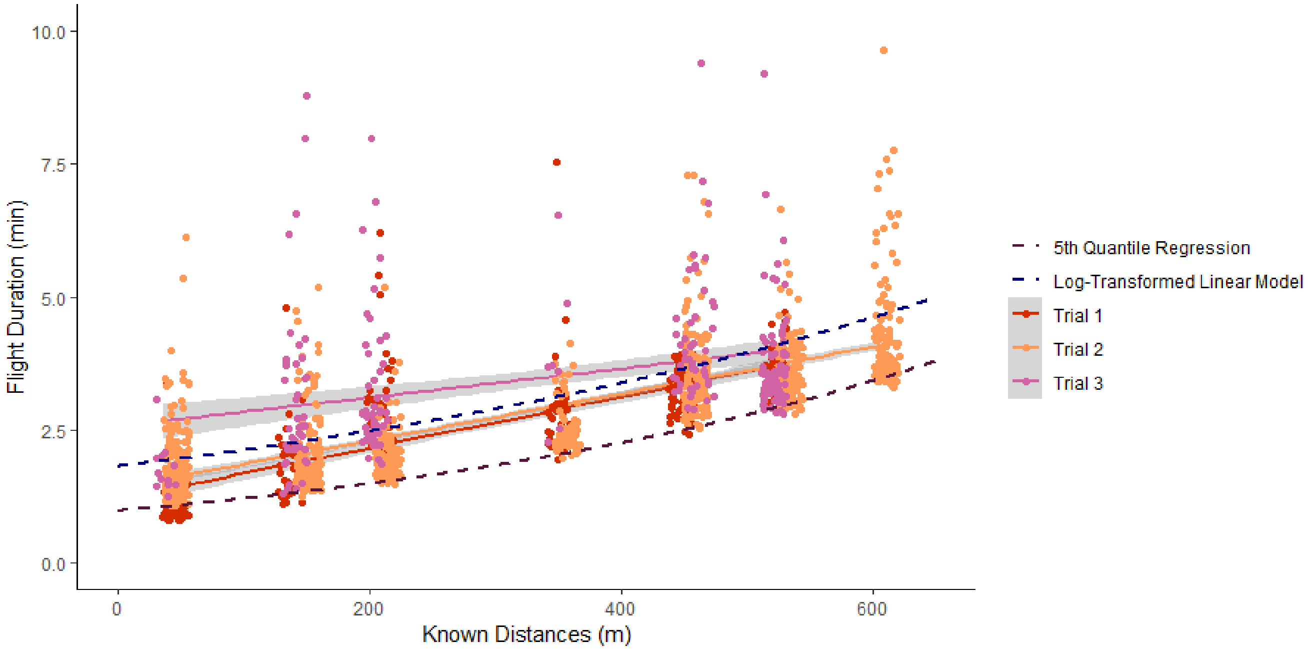

Figure 5: Individual bees' flight durations increased significantly with increasing distance for both models. Each circle (n = 1390) represents a measured flight duration for a given feeder visitation of an individually marked bee, where the feeders were at known distances and with different colors delineating trials. The X-axis is known distance in meters from the hive. The Y-axis is individual bee flight duration in minutes. The dotted blue line shows the Log-Transformed Linear Model as it bisects the spread of flight durations. At the lower bound of the data, the maroon dotted line shows the fit of the 5th Quantile Regression model.

Flight Duration, although Imprecise, is a Significant and Accurate Predictor of Distance Flown for Bees Visiting Feeders

When we compared the predictive performance of our two Calibration Models on our analysis population (n = 51 bees), we found that predictions from both models were in concordance with true distances. For the Log-Transformed Linear Model, the distance estimates for the analysis population, as output from the model, were significantly correlated with the real distances (Kendall's Rank Correlation: $\tau = 0.55$, $p < 0.001$; Figure 6A). These τ that are above 0 indicate a positive relationship, and, being closer to 1 than 0 indicate precision on the part of the model.

Importantly, this model underestimated distances flown for the closer Experimental Locations (c. 47-320 m), while also overestimating distances flown for the further away Experimental Locations (Figure 6A).

For the 5th Quantile Regression Model, the distance estimates for our analysis population, as output from the model, were significantly correlated with the real distances (Kendall's Rank Correlation: $\tau = 0.56$, $p < 0.001$; Figure 6B). The τ value again indicates a positive relationship between the real and estimated distances. This model overestimated distances for flight durations for every Experimental Location (Figure 6B). These overestimations are unsurprising, as a model that is based off the 5th quantile of data will make predictions in the 95th percentile.

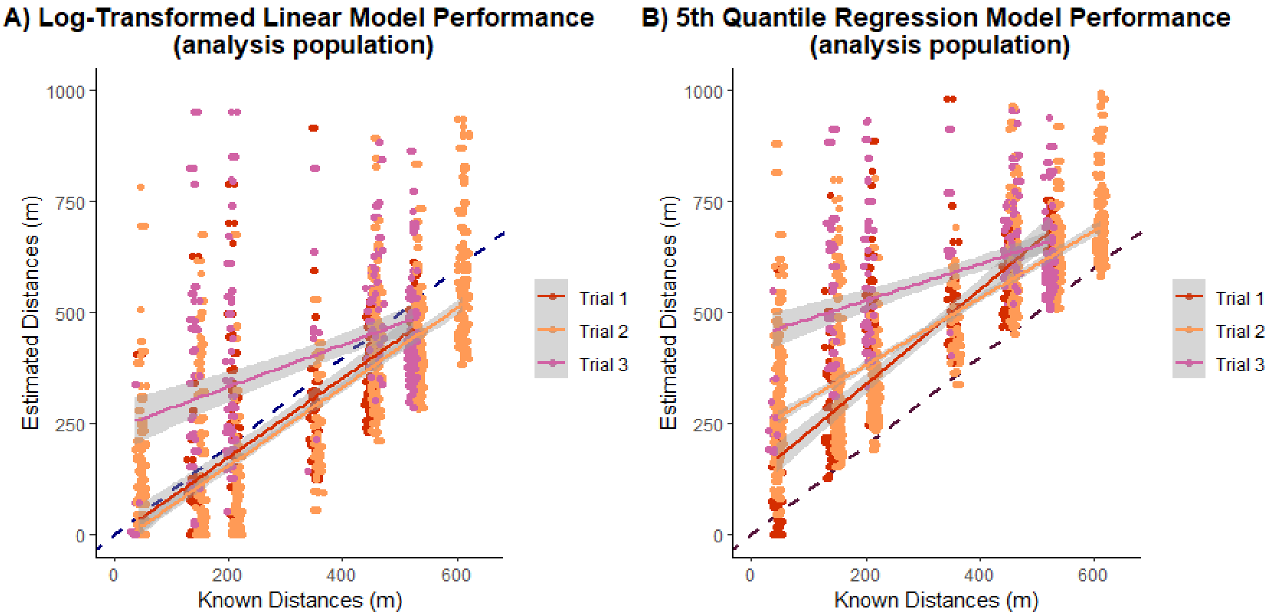

Figure 6: For the analysis population, both the Log-Transformed Linear Model (A, blue dashed line) and the 5th Quantile Regression Model (B, maroon dashed line) generate distance estimates that are significantly correlated to the actual distances. In both graphs, the X axis displays known distances of our Experimental Locations, and the Y axis shows estimated distances given that same bee's duration (circles). Dotted lines show the two models, with different colors denoting the trials.

The Hold-Out Sample Internally Validates Both Calibration Models

When applied to our randomly selected hold-out sample (n = 6 bees), both the Log-Transformed Linear Model (Kendall Rank Correlation: $\tau = 0.59$, $p < 0.001$; Figure 7A) and the 5th

Quantile Regression Model (Kendall's Rank Correlation: $\tau = 0.59$, $p < 0.001$; Figure 7B) produce distance estimates that are significantly correlated with the real distances. Importantly, these outcomes from our hold-out sample are very similar to those seen in our analysis population, indicating that the models perform well for both the data upon which they were trained (analysis population) and data upon which they were not (hold-out sample).

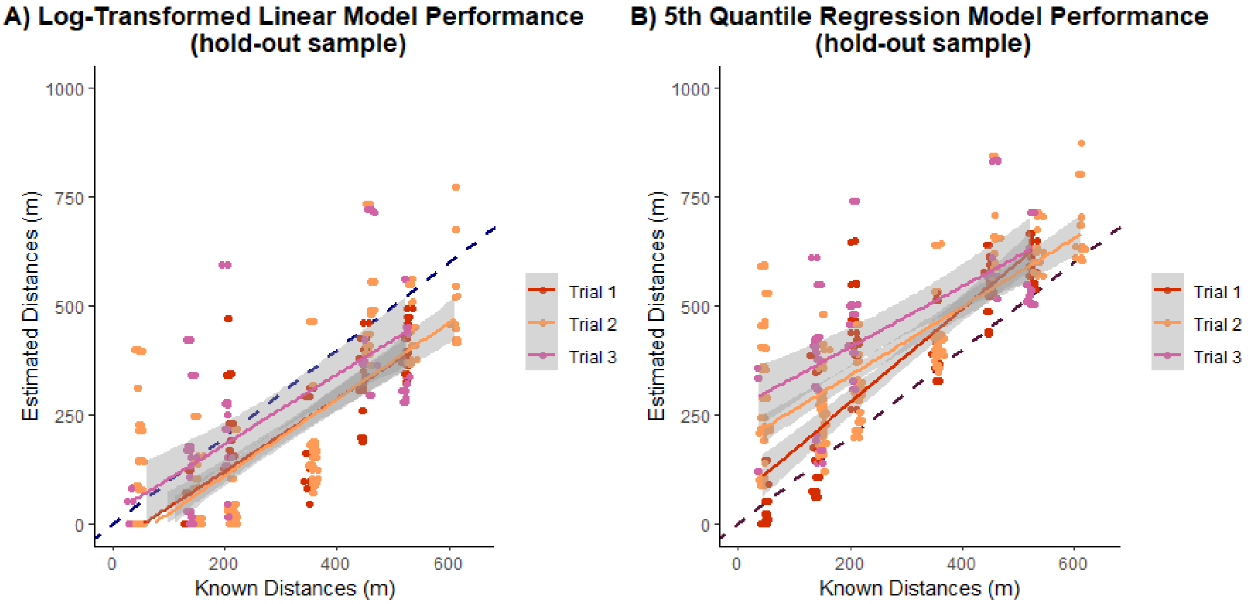

Figure 7: For the hold-out sample, both the Log-Transformed Linear Model (A, blue dashed line) and the 5th Quantile Regression Model (B, maroon dashed line) generate distance estimates that are significantly correlated to the actual distances. In both graphs, the X-axis displays known distances of our Experimental Locations, and the Y-axis shows individual estimated distances given that same bee's duration (circles). Dotted lines show the two models, with different colors denoting the trials.

There is a Non-Significant Relationship between Flight Durations and Waggle Run Duration for Freely Foraging Bees

We found a non-significant, negative linear relationship between waggle run durations and flight durations for bees freely foraging and recruiting in the landscape (simple linear model: $R^2 = 0.073$, $F = 13.48$, $df = 171$, $p < 0.0001$; Figure 8). While the p-value we calculated indicates a significant relationship, such a small R^2 value shows that this relationship was incredibly weak. For validation bees, for each 0.5 sec (approx.. 325 m) of increase in waggle run duration, flight durations decreased by 5.9 minutes (approx..780 m) based upon this relationship. Overall, the bees in the

Validation Trials had longer flight durations (mean = 19.2 ± 10.5 minutes) than bees that foraged upon feeders (mean = 2.94 ± 1.5 minutes).

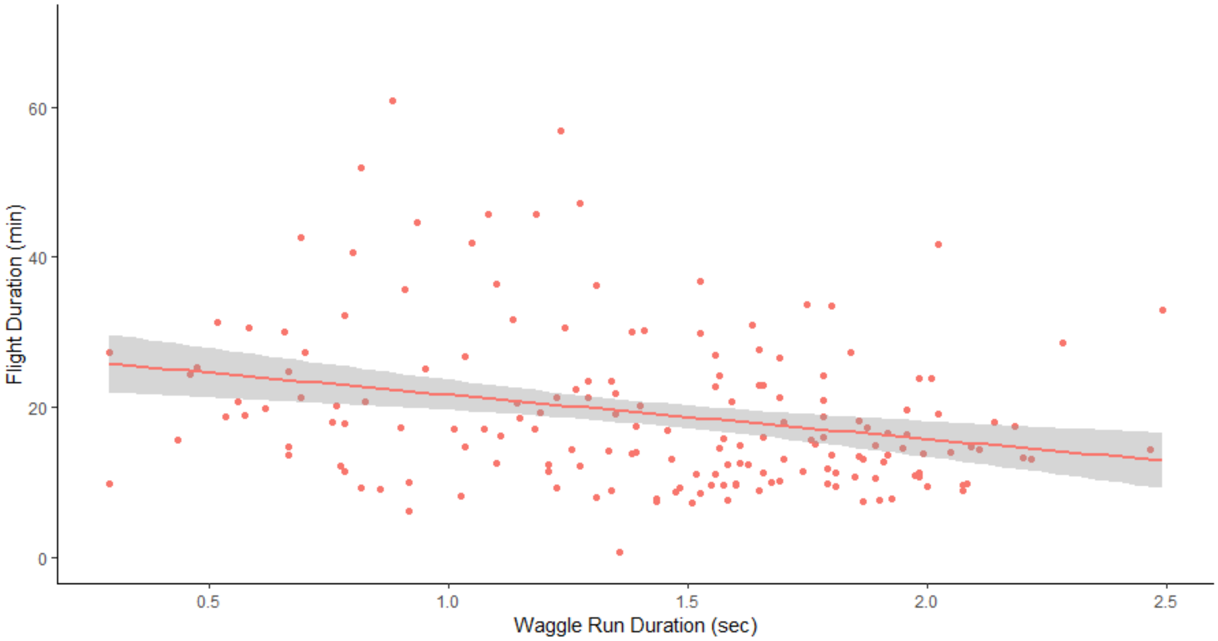

Figure 8: Flight durations for freely foraging bees decrease with increasing waggle run duration. The X-axis displays waggle run duration in seconds, and the Y-axis shows flight durations in minutes. Each circle represents an individually marked bee's foraging trip, from which we collected the two pieces of data (waggle run duration and flight duration).

Flight Duration Distance Estimates are Negatively Correlated with Waggle Dance-Distance Estimates for Freely Foraging Bees

We found flight distances, as estimated from the flight duration of marked bees using our Calibration Models, were negatively correlated with the communicated distances, as estimated from the waggle dance durations from the same bee: this was true with both our log transformed linear Calibration Model distance estimates (Kendall Rank Correlation: $\tau = -0.17$ $p < 0.001$; Figure 9A) and our 5th Quantile model distance estimates (Kendall Rank Correlation Test: $\tau = -0.17$, $p < 0.001$; Figure 9B).

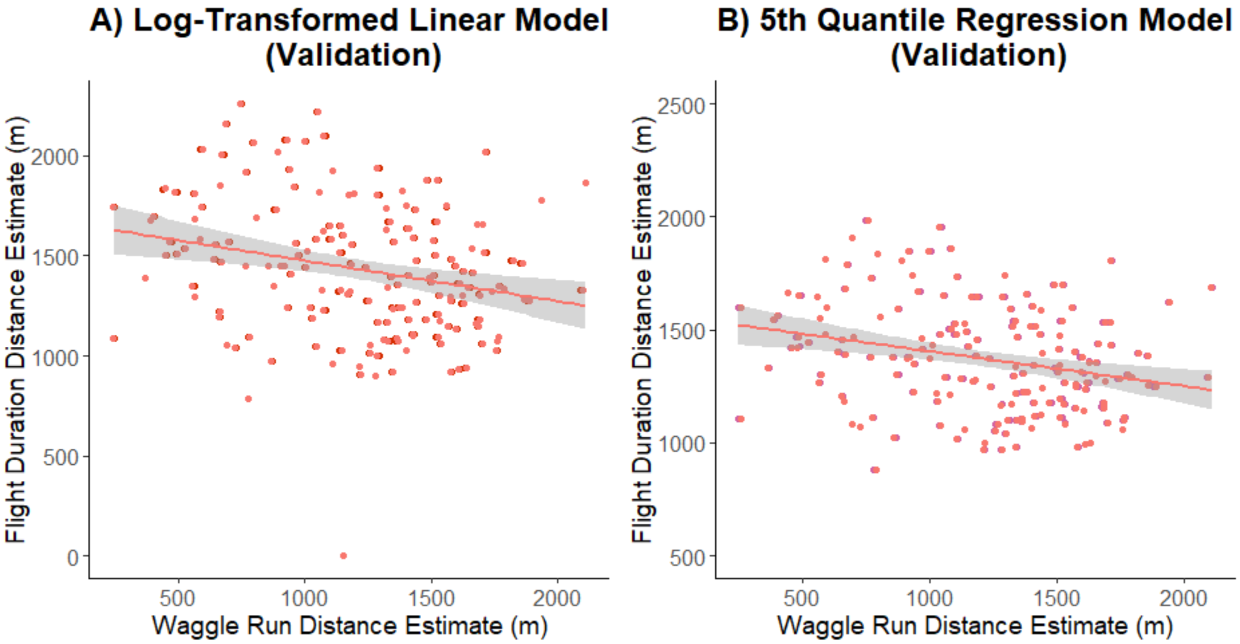

Figure 9: Both Calibration Models, the Log-Transformed Linear Model (A) and the 5th Quantile Regression Model (B), produce distance estimates that are negatively correlated with distance estimates made with waggle dance data for the same individual bees. In both plots, the X-axis shows the waggle run distance estimate, where we converted waggle run durations into communicated distance using a previously published calibration. The Y-axis shows the distance estimates from flight durations, where we converted flight duration into a distance estimate using either the Log-Transformed Linear Model or the 5th Quantile Regression Model. Each circle represents a foraging trip made by an individually marked bee.

Dividing Up by Nectar versus Pollen Removes maintains the Non-Significant Relationship Between Flight Duration and Waggle Run Duration

We found that there was no significant relationship between waggle run duration and flight duration when we separated these data by forage type (Kendall's Rank Correlation for nectar foragers: τ = -0.1 p = 0.11; Kendall's Rank Correlation for pollen foragers: τ = 0.09, p = 0.33; Figure 10). We generally saw that pollen foraging durations (mean: 24.5 ± 11.8 minutes; median: 21.3 minutes) were longer than nectar foraging durations (mean: 16.7 ± 8.8 minutes; median: 14.1 minutes; Figure 10). Conversely, for the same bees and across the same foraging trips, waggle run durations for pollen foragers were shorter (mean = 1.11 ± 0.5 s) than for nectar foragers (mean = 1.60 ± 0.42 s). These differences between foraging groups were found to be significant from a log-rank test for both flight duration (Chisq = 18.5, Df = 1, p < 0.001) and waggle run duration (Chisq: 18.8, Df = 1, p < 0.001; data not shown).

These differences translated to distance estimates made with the Calibration Models: pollen foragers had a mean of 1599.3 ± 313.2 m from the Log-Transformed Linear Model and a mean of 1499.9 ± 236.6 m from the 5th Quantile Regression Model. Flight duration-distance estimates for nectar foragers, on the other hand, had a mean of 1353.2 ± 310.9 m from the Log-Transformed Linear Model and a mean of 1311.4 ± 247 m from the 5th Quantile Regression Model. Waggle dance-distance estimates differed between foraging modalities (pollen vs. nectar), with pollen foragers having a mean waggle dance-distance estimate of 962.2 ± 414.5 m and nectar foragers having a mean waggle dance-distance estimate of 1322 ± 352.2 m.

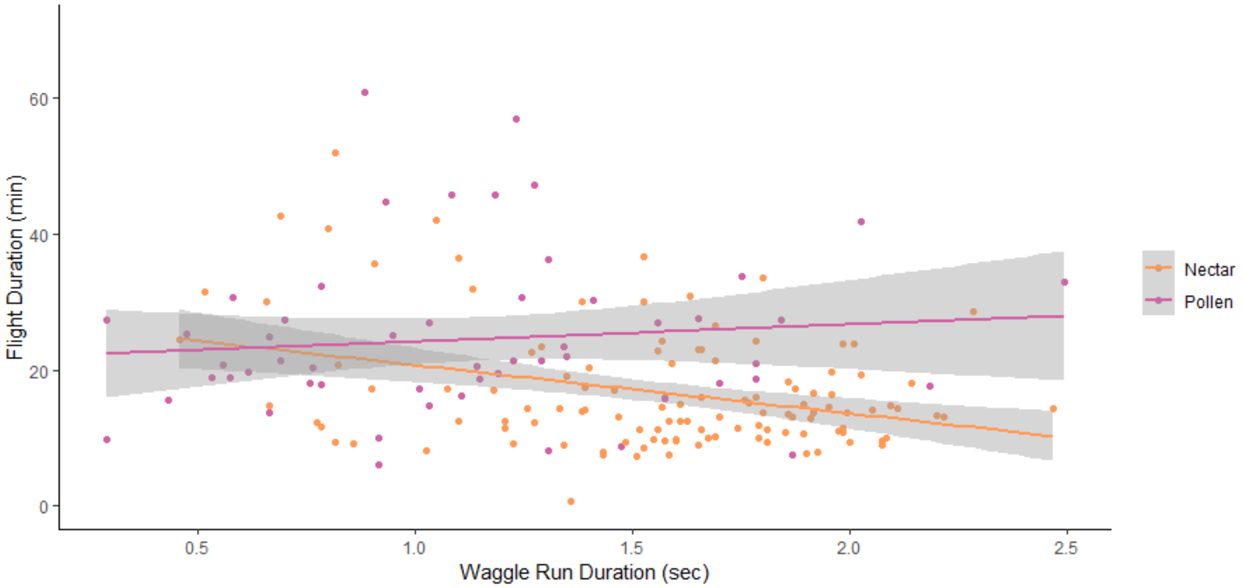

Figure 10: Flight durations for bees foraging upon pollen are higher than those of bees foraging for nectar. The X-axis displays waggle run duration in seconds, and the Y-axis shows individual flight durations in minutes. Each circle represents a flight for an individual bee, with the different colors showing the foraged resource (nectar or pollen).

Discussion

Here we have shown in a Calibration experiment that flight duration is a significant predictor of foraging distance for bees trained to drink from artificial feeders. This significance was maintained with both Calibration Models, the Log-Transformed Linear Model and the 5th

Quantile Regression Model. Importantly, both models were able to predict the foraging distance accurately and significantly from the flight duration for a hold-out sample, a random selection of six bees that were not used to produce either model. We have also shown in a Validation experiment that comparing distance estimates from waggle runs and distance estimates from flight durations unexpectedly produced a non-significant relationship, with a slight negative trend. Although we do not know from these data the reason behind this unexpected outcome, it may be that for freely flying bees foraging naturally in the landscape, the impacts of other unknowns, like handling time and recruitment thresholds, add confounding variables that make our interpretations unclear. Therefore, although the Calibration Models may be used for large-scale field trials to estimate foraging distances from many flight durations, it is important to remember that real world predictions will be noisy, usually overestimated for longer distances (and occasionally underestimated for shorter distances), and complicated if the forager is also a dancer.

Flight Duration and Distance have a Significant, Positive Relationship

We showed that, for bees trained to feeders, flight duration significantly increased with increasing distance (Figure 5). This was true for both Calibration Models: the Log-Transformed Linear Model found that, when back-transformed to our original scale, flight duration increased by 1.8 minutes per 100 m, and the 5th Quantile Regression Model found that flight duration increased by 0.98 minutes per 100 m (Figure 5). These durations possessed a large, upward spread for every Experimental Location, with little variation on the lower bound of the data (Figure 5).

While this tight lower bound in the data could have arisen from our data cleaning, the data that were removed represented less than 0.3% of our total dataset. We timed how long it took for bees to drink from a feeder and calculated the median crop fill time as 43.5 s (Figure 4). The Experimental bees trained to feeders were required to perform an outward flight, drink from the feeder, and perform a return flight. We therefore reasoned that any marked bee (i.e., the bees trained to the feeders) whose trip duration was less than 43.5 s was likely doing something other than foraging, such as performing an evacuation flight (Ribbands 1949, 1964; Winston 1991). Therefore, we felt we were justified using 43.5 seconds as a conservative, data cleaning cut-off, especially combined with the fact that these removed data comprised such a small percentage of our overall dataset.

Importantly, these crop fill data also underscored how quickly bees drinking from feeders were likely to complete a foraging roundtrip. This expediency is in contrast with the greater amount of time that honey bees would likely take to fill a crop, even partially, from flowers. Previously it was shown that bees must visit between 6 and 119 flowers within a single foraging bout before returning to the hive, a range that varies with flower type: bees visit 14-20 lavender flowers, 24-32 oregano flowers, 18 dandelions, 14-19 poppies, and 800 florets of white clover to gather the nectar and sometimes pollen that they need (Ribbands 1949; Goodwin et al. 2011; Hennessy et al. 2021). These visits can take 3.8-44.1 minutes, depending on flower type (Ribbands 1949; Goodwin et al. 2011; Hennessy et al. 2021). In contrast, drinking *ad libitum* from an endlessly supplied, artificial feeder allows bees to have the quickest possible crop fill time, as handling time becomes negligible with no actual flowers to handle. Foraging honey bees will partially fill their crops with nectar (or, in the case of the Calibration bees, sucrose solution) in order to maximize energy efficiency (net energetic gain/energy expenditure), as heavier loads require more energy to transport home (Schmid-Hempel et al. 1985; Schmid-Hempel 1987). This cost-dependent crop filling occurs at both short and long foraging distances (Schmid-Hempel et al. 1985; Kacelnik et al. 1986; Schmid-Hempel 1987). We would expect the experimental bees also to engage in partial crop filling as they would in the field, with the difference being that they can do so very efficiently and with relatively little variation between bees, at least compared across bees foraging on different flower species. Therefore, the fact that both models display a linear relationship is unsurprising, where actual handling/crop fill time is nearly constant and where flight durations should increase with increasing distance.

Weather may also play a role in how long a foraging trip will take. High-wind speeds increase handling time and reduce the number of visited blossoms (Hennessy et al. 2021), although this impact might also be minimized with an artificial feeder that does not bob in the wind. Because nectar flow rates are higher when ambient temperatures are higher, bees optimize nectar intake by foraging in sunny locations or by increasing body temperature while in the shade (Stabentheiner and Kovac 2016). In our Calibration experiment, we kept our feeders shaded with a large camping tent, and we only performed the trials on warm and sunny days. We did informally examine the potential impact of weather by assessing temperature and wind speed data for the different trials and days within the Calibration Experiment, but we found very little change in flight durations from day-to-day and hour-to-hour, indicating that the effects of weather may be negligible for the bees in this set-up.

In addition to our more standard Log-Transformed Linear Model, we also opted to analyze our Calibration data using a 5th Quantile Regression Model. We chose this additional analysis to add another layer of conservatism to potential distance estimates. Using the 5th Quantile Regression Model, we can therefore observe distance estimates that come from the upward spread of flight duration data, in this case the 95th quantile. Indeed, most predictions made by the 5th Quantile Regression Model range between 317 and 622 m (Figure 6B), while most of the predictions made by the Log-Transformed Linear Model range between 30 and 438 m (Figure 6A).

Additionally, when generating distance estimates beyond the range of our Experimental Locations, the behavior of either Calibration Model is unknown because their training data was limited by our maximum distance (611 m). This limitation is present when our models are applied to our Validation dataset, which, according to the waggle run distance estimates, has many points beyond 611 m. Another limitation with these models is that they were internally validated by a small holdout sample. This internal validation could be made more robust via bootsrapping, or through an external validation by other researchers.

Both Calibration Models Generate Significant and Accurate, but Imprecise, Distance Predictions for Both Training Data and Hold-out Sample

The results of the Kendall's Rank Correlation for our analysis population for both Calibration Models (Long-Transformed Linear Model and 5th Quantile Model) demonstrated that the models predicted, from the measured durations, flight distances that were in concordance with the actual flown distances (Figure 7). Additionally, the τ value, an output from the Rank Correlation that indicates the strength of the relationship between the ranked variables, was similar for both models ($\tau = 0.55$ for the Log-Transformed Linear Model; $\tau = 0.56$ for the 5th Quantile Regression Model). In other words, both models performed significantly and similarly.

Crucially, when we used Kendall's Rank Correlation with our hold-out samples, the bees that were not used to train our predictive models, we also found that both of model predictions were significantly, positively correlated with the real measured distance (Figure 7). Once again, the τ values were similar ($\tau = 0.59$ for the Log-transformed Linear Model; $\tau = 0.59$ for the 5th Quantile Regression Model). Ultimately, these results provide an internal validation of the experiment and indicate that both Calibration Models may also be used for future data to unknown distances.

The key difference between the models lies in the way they make predictions from the training data. The Log-Transformed Linear Model is based upon the average flight durations observed at each Experimental Location. This enabled the model to produce distance estimates that represent the center of the data, while having a large upper and lower range, generating both over- and underestimates of distance (Figures 6A and 7A). In contrast, the 5th Quantile Regression Model is based on the minimum amount of time a bee needs to fly to a known location. This allows the model to make distance estimates that are in the 95th percentile and are therefore largely overestimated. In other words, the 5th Quantile Regression Model shows the furthest possible distance that a bee could travel for that flight duration. This is especially evident in the large upward spread of prediction data (Figures 6B and 7B).

Overall, the large range in distance predictions from each Calibration Model is reflective of the fact that flight duration is a messy predictor of distance. Even in a controlled foraging situation like a feeder, bees vary in flight durations for a given distance (Figure 5), between different bees and even most likely for the same bee making successive trips to the same location. As honey bees become more familiar with a particular resource location, they will optimize their flight route, leading to quicker, repeat trips over time (Capaldi et al. 2000). Additionally, there may be inter-individual differences in resource-familiarity that leads to one individual having quicker initial flights, while another bee might need more time to fine-tune her route. Future investigations should examine the impact of learning and flight experience on trip durations and how these might differ across and within bees.

Given the similarities in the predictive abilities between the Calibration Models, either may be used for distance predictions, with the 5th Quantile Regression Model showing the greatest possible distance and the Log-Transformed Linear Model predicting more average distances based on flight duration. Additionally, one should remember that bees drinking from feeders are extremely efficient: for these bees, each measured trip duration involves an outbound flight, a (partial) crop fill from a feeder that is as quick as possible with negligible handling time, and an inbound flight. If that same trip duration is observed for a bee that is working with actual flowers, a larger portion of that overall duration will not actually be in flight. In other words, our Calibration will, when applied to most cases of freely flying bees, generate a maximum possible foraging distance estimate for a given duration, an overestimation that may be even greater with the 5th Quantile Regression Model. Therefore, from a risk assessment standpoint, where one is determining the foraging range that should be kept free or reduced from contaminants, these overestimates will be beneficial in determining if most bees from a colony are staying within a set area.

There is a Negative, Non-Significant Relationship Between an Individual's Waggle Run Duration and Flight Duration for Freely Foraging Bees

In the Validation trials, we were able to compare the flight durations for individually marked, freely flying bees to their performed waggle run durations, which communicated the distance at which they actually foraged. We found, surprisingly, and in contrast to our expectations, that flight durations were not significantly related to waggle run durations (Figure 8). Individual flight durations were larger for shorter waggle run durations, which communicate a nearby foraging location, and individual flight durations were shorter for longer waggle run durations, which communicate further away foraging locations. This non-significant, inverse relationship also was evident when we converted durations (both waggle and flight; Figure 9), which is unsurprising given the underlying data that we measured (Figure 8). In general, we did find that average flight durations from freely foraging bees were much longer (19.2 ± 10.5 minutes) than average flight durations in our Calibration Experiment (2.94 ± 1.5 minutes). Of course, part of the increased duration is likely from the increased floral handling time compared to feeder drinking: our feeder training methodology allowed us to observe the relationship between flight duration and distance by greatly reducing the confounding variables associated with foraging upon natural flowers, and adding these variables back into the mix in our Validation Experiment may have added a layer of noise to our data interpretation. However, even this is not entirely explanatory of the lack of a significant relationship that we found in our Validation result.

Although there are many ways in which previous work has estimated flight distances from foraging bees, including harmonic radar and mark/recapture (Gary 1971; Seeley 1995; Riley et al. 1996; Capaldi et al. 2000), waggle dance decoding is our current gold standard (von Frisch 1967; Beekman and Ratnieks 2000; Beekman et al. 2004; Couvillon et al. 2014a, a; Steele et al. 2022; Ohlinger et al. 2024). Importantly, waggle run duration is known to have a positive relationship with the distance to the resource (von Frisch 1967; Seeley 1995; Beekman and Ratnieks 2000) that accrues linearly with increasing distance (Schürch et al. 2013, 2016b, 2019). Indeed, waggle run durations have been used to estimate bee foraging distances in the landscape in the many decades since Karl von Frisch decoded the dance language (Beekman et al. 2004; Couvillon et al. 2012; Schürch et al. 2019; Carr-Markell and Spivak 2021; Steele et al. 2022). Given that waggle run duration increases linearly with distance, and our Calibration experiment showed a significant, positive relationship between flight duration and distance, why might it be that we see a negative relationship between flight duration and waggle run duration?

One explanation for the unexpected result may be an actual function of using waggle dances in the first place: all the Experimental Validation bees were, by definition, ones that not only took a foraging trip, but that also performed a recruitment dance. These bees may have already optimized their flight routes by the time they danced (and therefore appeared in our Validation dataset). Each bee possesses a dance threshold that varies between individuals (von Frisch 1967; Seeley 1995), but in general, across bees, the more a bee visits a particular, high-valued resource and becomes assured of its profitability, the higher her propensity to dance will be (von Frisch 1967; Seeley 1995; Couvillon et al. 2015a, 2023, 2024). Then, in visiting this resource multiple times, a bee's flight path will become more efficient (Capaldi et al. 2000), most likely before she even begins to dance. Perhaps Validation bees are only present in our data once they are exceptionally quick in their flight, presenting a duration that, even with the noise of handling time, is speedy compared to the actual foraging distance. Additionally, the valuation of a resource against flight distance (and the decision to recruit) may also vary between nectar and pollen.

Honey bees only dance for highly valued resources and, because of the cost of flight, honey bees prefer closer resources when both close and far resources provide the same sugar reward (Seeley 1986; Al Toufailia et al. 2013; Couvillon et al. 2014a). But, when the far away resource produces a higher sucrose reward, the bees will evaluate if the increased nutrition makes the longer trip worthwhile (Seeley 1986, 1994; Couvillon et al. 2014a). Therefore, if the energy gained from the nectar reward is high enough to outweigh the cost of the flight, the bees will perceive the resource as higher quality, continue exploiting it, and, if it is sufficiently higher quality, be more likely to recruit their nestmates via the waggle dance (von Frisch 1967; Seeley 1986, 1994). Additionally, we know that bees partially fill their crops depending on flight distance (Schmid-Hempel et al. 1985; Kacelnik et al. 1986; Schmid-Hempel 1987). Taken together, when honey bees forage at far distances, it is almost always because there is no other high quality forage closer to the hive (von Frisch 1967; Seeley 1995; Couvillon et al. 2014b, a; Steele et al. 2022; Ohlinger et al. 2022b). Because bees have a lower threshold of "goodness" closer to the hive based on net energy expenditure, could handling time efficiency also be a factor in resource valuation? If a flower more readily supplies pollen or nectar, or a bee does not need to visit as many flowers to fill her crop, it may reduce the amount of energy expended by the bee while foraging. Overall, this need for efficiency may lead to bees preferring to forage upon more efficient resources, especially when further away and energy expenditures are already higher.

When Split by Foraged Resource, Flight Durations for Freely Foraging Bees maintain Non-Significant Relationship with Flight Distance

We again found no significant relationship (positive or negative) between flight duration and waggle run duration when data were split by resource type of nectar or pollen (Figure 10). One should note that the lack of relationship between flight duration and distance flown, when split by resource foraged, may be due to a reduction in statistical power. Our overall Validation analysis was performed on the 173 bees for whom we were able to obtain both flight durations and waggle dances. These 173 bees represented 55 pollen foraging bees and 118 non-pollen, presumably nectar, foraging bees. Visually, the negative relationship for the total dataset may also be a function of pollen foragers having higher flight durations for shorter waggle dance distance estimates (i.e., clustering in the upper left hand portion of the graph; Figure 10), while nectar foragers had lower flight durations but traveled further based on waggle dance estimates (i.e., clustering in the lower right hand portion of the graph; Figure 10).

We did however see both a difference in flight duration between the foraging modalities and a difference in waggle run duration between the foraging modalities. Pollen foraging duration (mean: 24.5 ± 11.8 minutes) was significantly longer than nectar foraging duration (mean: 16.7 ± 8.8 minutes; Figure 10). Interestingly, pollen waggle run durations were significantly shorter (mean = 1.11 ± 0.5 s) than nectar waggle run durations (mean = 1.60 ± 0.42 s). These waggle run durations translate to a mean foraging distance of 962.2 ± 414.5 m for pollen foragers and 1322 ± 352.2 m for nectar foragers. In other words, pollen foraging bees took longer but tended to forage closer by (as indicated by decoded waggle dances), whereas nectar foraging bees took less time but tended to forage further away (as indicated by decoded waggle dances). This agrees with previous work that found that honey bees will forage for nectar at distances 14% further than for pollen, and that nectar foraging distances are greater than pollen foraging distances 85% of the time (Ohlinger et al. 2022b).

Our results suggest that there is a difference between pollen and nectar collection and how it interacts with flight durations and foraging distances. These differences may be due not just to handling time, but potentially other factors like aerodynamics. Pollen is carried outside of the honey bee's body, in large clumps on her corbiculae, while nectar is carried within her crop (Winston 1991; Seeley 1995). Bumblebees that carried pollen in their corbiculae were found to be more stable, but less maneuverable than bumblebees that carried nectar in their abdomen (Mountcastle et al. 2015). Interestingly, bumblebees with pollen loads had a higher median flight speed when winds were unsteady, but were hindered by their loads when attempting to land on an unsteady flower (Mountcastle et al. 2015). Honey bees may also be affected by this tradeoff of stability vs maneuverability, in addition to other, unknown impacts of floral resource type on flight duration.

The validation data suggest that there are several factors that may impact the efficacy of flight duration-distance estimates; however, the direct effects of these factors are, as of yet, unknown. One of these factors, handling time on natural flowers, is incredibly varied, perhaps because of the great diversity of floral types, and it is nearly impossible to have generalized floral handling constant. It would be useful to have a better understanding of how bee-resource interactions impact foraging time, especially as it pertains to flower size, nectary differences (fast-flow vs slow-flow and nectar contents), and floral resource type (handling pollen vs nectar). Additionally, understanding the aerodynamics of flight, especially with pollen or nectar loads or in different weather conditions, may lend insight into the variation we see in flight durations.

There are some inherent biases that waggle dance decoding may introduce to flight duration data. Bees that perform a recruitment dance are inherently more familiar with a resource location, and therefore a more efficient forager of it (von Frisch 1967; Seeley 1995; Capaldi et al. 2000; Couvillon et al. 2015a, 2023, 2024). Future work should investigate if flight time efficiency increases with increasing familiarity with a resource. Additionally, bees will only recruit for high-value resources, which are evaluated, in part, by their efficiency. Because handling time can account for a large portion of a bee's foraging duration, future work should assess if resources with a shorter handling time will lead to a greater waggle dance propensity. Ultimately, because of these confounding variables that waggle dance data introduce, our calibration remains unvalidated for freely flying bees. It may be possible for flight duration to be measured against another method of estimating distance, such as harmonic radar.

Conclusions

When estimating honey bee ranges on organic farms, one must remember that every method of tracking honey bee foraging distance has its own challenges and limitations. To track honey bees with harmonic radar, a passive transponder is glued to the thorax of a departing forager, which will then re-radiate a harmonic of a radar signal, allowing researchers to map flight trajectories (Riley et al. 1996). However, harmonic radar has a limited range (50-250m), signals may get confused in a more cluttered landscape, and the transponders may contribute to drag or be too heavy for the bees to travel longer distances (Riley et al. 1996; Milanesio et al. 2016). Although a transponder weighs less than an average load of pollen or nectar, the added bulk may still be enough for bees to arbitrarily shorten their flights to lessen the caloric expenditure (Capaldi et al. 2000). Further, the transponders are too tall for bees to be able to re-enter their hive, meaning that studies that require both flight tracking and in-hive monitoring could not use this method (Capaldi et al. 2000).

Another method of estimating bee flight distance is mark-recapture: bees are given a distinguishing paint-job, either in the hive or in the field, and then recaptured or observed in the landscape or at the hive, respectively (Levin 1961; Gary 1971; Gary et al. 1972; Seeley 1995). These markings could be fluorescent dust, paint mark, number tag, magnetic metal label, or a genetic marker (Levin 1961; Gary 1971; Seeley 1995). Mark-recapture can be limiting because researchers may only search in the field where they assume the bees will be, thus making the data non-random and hugely biased, with extremely low efficiency (Seeley 1995).

While decoded waggle dances are our current gold standard in mapping honey bee foraging, this method also possesses limitations. Study colonies must be housed in specialized, glass-walled hives that cannot be placed in a field, and decoding these dances is incredibly labor and time intensive (Couvillon et al. 2012). Additionally, because bees only dance for highly-valued resources, the snapshot of foraging patterns that the waggle dance analysis produces is limited to this subset of highly valuable resources (von Frisch 1967; Seeley 1995; Couvillon 2012).

Finally, utilizing an automated hive entrance detection system to collect flight durations offers advantages over these previous methods in that it is less labor and time intensive and captures a wider breadth of foraging data (Penaloza-Aponte et al. 2024; Brandt et al. 2025). However, as we have shown, this method is most accurate for bees foraging on artificial feeders, where the extraneous variables associated with foraging upon natural flowers are removed. When flight duration is used to predict distance for bees that also recruit with waggle dances, the distance estimates are negatively correlated with communicated distance. While we do not yet know why the results of the Validation Experiment do not align with those of the Calibration Experiment, the differences may be explained by the fact that our validation data are from a sub-set of foragers that may have optimized flight routes or chosen the most efficient resource possible. To understand how these factors may affect the flight durations of recruiting bees, the flight durations of bees leading to their first waggle dance should be investigated. Taken together, these results demonstrate that flight duration may be used as a proxy for distance, but with the caveat that any distance predictions will likely be greatly overestimated most of the time, especially if the 5th Quantile Regression Model is used. However, if flight durations being used to determine if the USDA standards for organic certification are realistic, having an overestimated, conservative distance estimate is valuable and may lead to updated requirements.

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