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Markerless tracking of bumblebee foraging allows for new metrics of bee behavior and demonstrations of increased foraging efficiency with experience

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Abstract – Bumblebees have become model organisms for cognitive ecology and social learning. Quantifying the foraging behavior of free-flying bees, however, remains a methodological challenge. We describe and provide the code for a method of studying bee free flying foraging behavior using the open source neural-network based markerless tracking software DeepLabCut. From videos of bees foraging in an arena we trained a neural network to accurately track the position of each bee. We then used this approach to study foraging behavior and show that the ratio between flying time and flower visiting time decreases over repeated foraging bouts, indicating increasing efficiency of bee foraging behavior with experience. Visit durations, a laborious metric to measure by hand, were significantly shorter on flowers that had previously been visited. This experiment illustrates the usefulness of DeepLabCut for objective quantification of behavior, and in this case study shows that previous experience increases bee foraging efficiency.

DeepLabCut / bumblebee / foraging / behavior / neural network

1. INTRODUCTION

Bees have long been used as model systems for exploring questions in ecology, evolutionary biology, and psychology (Darwin and Huxley 1859; Frisch 1914; Renner 1960; Bloch and Grozinger 2011; Elekonich and Roberts 2005; Lemanski et al. 2019; Raine et al. 2006; Srinivasan 2010). The methods used to study bee foraging behavior have included field surveys, laboratory flight arenas, restrained bees in proboscis extension response assays, and computer modeling (Frisch 1914; Kuwabara 1957; Ratnayake et al. 2021; Scheiner et al. 2013;

Toshack and Elle 2019). A central challenge of studying free-flying bee foraging has been measuring and quantifying three-dimensional behavior over a large and visually complex area. Radar is technically demanding, but can be used to track entire bumblebee foraging bouts in the wild (Woodgate et al. 2016, 2017). Another approach is to use constrained foraging arenas and limit the floral choices which allows for easy metrics of which flowers are visited, but leaves tracking visit lengths and flight times between flowers challenging to quantify. Most studies are therefore required to focus only on a few bee behaviors such as which flowers are visited and in what order (Pasquaretta et al. 2019; Sontner et al. 2019). This traditional method of quantifying behavior is limited in its ability to study complex behaviors and relies heavily on

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human observation, which has associated issues of observer bias (Crall et al. 2015; Dankert et al. 2009; Simons and Chabris 1999).

Recently there has been an increasing use of automated tracking software for quantifying bee behavior. Motion tracking software can be used to analyze videos in a time efficient manner that reduces human bias and has been used successfully in a variety of bee species to study pollination, flight behavior, and nest selection (Ratnayake et al. 2021; Knauer et al. 2022; Rodriguez et al. 2022; Richter et al. 2023; Sun and Gaydecki 2021). However, these implementations of motion tracking software are limited by their technological complexity and inability to capture entire foraging bouts. Many labs, therefore, continue to track bee behavior without the assistance of automated video analysis (Nityananda and Chittka 2021; Siviter et al. 2021). The currently available motion tracking tools are slow to be implemented in many bee behavior experiments because of their technical complexity, time consuming analysis process, or their inflexibility to being tacked on to existing systems.

While some labs develop and use in-house software packages, there are also many motion tracking tools available for use online. User-friendly software packages like Tracker (version 6.0.3; <http://physlets.org/tracker>) or DLTdv are easy to implement into existing experimental setups, but their analyses must be constantly monitored and are thus time consuming (Fernández et al. 2017). We trial ran DLTdv8's deep learning analysis and found automated tracking for our data very error prone. Other software systems like Flydra can be accurate but require multiple cameras with no option to only track 2D flight paths. This additional equipment and computational need may limit the cost-effectiveness for some users. (Straw et al. 2011). In our study we used the markerless pose estimation software DeepLabCut from the Mathis Lab (Mathis et al. 2018), which we found balanced ease of use, accuracy, and time efficiency. DeepLabCut was originally designed to track the positioning of body parts in neuroscience experiments (Mathis et al. 2018) and has since been used successfully in experiments to track body positioning of bees,

including carpenter bees *Xylocopa varipuncta* (Burnett and Combes 2023), honeybees, *Apis mellifera* (Kohnno et al. 2023; Gascue et al. 2022), and buff-tailed bumblebees, *Bombus terrestris* (Richter et al. 2023). We propose that DeepLabCut also has enormous utility for studying flower selection and visit durations by bumblebees in the types of experimental setups common in bumblebee cognition research labs (Jones et al. 2023; Jones and Agrawal 2016; Dawson et al. 2013; Richman et al. 2021; Wolf and Chittka 2016). Given the untapped potential of motion tracking software to quantify behavior while bees visit different types of flowers, we used DeepLabCut to investigate how bees' increase their foraging efficiency with experience using multiple metrics.

It has been well documented that foraging efficiency in honeybees and bumblebees increases with experience (Ohashi et al. 2007; Saleh and Chittka 2007; Lawson et al. 2017). The use of consistent foraging routes, known as traplining, is one mechanism by which bees can optimize foraging bouts (Lihoreau et al. 2010, 2012; Thomson et al. 1997). Many studies have looked at other metrics of efficiency beyond traplining, and found that with more foraging experience, total bout duration decreases, flight length decreases, and overall resource collection increases (Klein et al. 2019; Woodgate et al. 2017). Foraging efficiency has also been studied at a smaller scale by looking at handling time for individual flowers (Lawson et al. 2017). Many of these metrics are time-consuming and attentionally demanding to track by hand, and may be particularly vulnerable to error, thus presenting an ideal opportunity for the application of motion tracking video analysis.

In this paper, we describe a novel application of the open-source software DeepLabCut (Mathis et al. 2018; Nath et al. 2019), using it in a laboratory setting to assess foraging efficiency over multiple foraging bouts in free-flying bees. In accordance with the previous literature about foraging efficiency in bumblebees (Ohashi et al. 2007; Saleh and Chittka 2007; Lawson et al. 2017; Klein et al. 2019; Woodgate et al. 2017), we predicted the ratio of time spent visiting

flowers versus in transit time between flowers to increase with foraging experience. We tested this prediction using bumblebee behavioral experiments in the laboratory and markerless motion tracking with DeepLabCut. We report on bumblebee foraging efficiency and the performance of DeepLabCut as a tool for this type of analysis.

2. METHOD

Foraging arenas consisted of a 117 cm × 71 cm × 34 cm plywood box with a plexiglass top. Within the arena was a rectangular array of 12 artificial flowers, 17.5 cm apart. Each flower consisted of 2.0 cm × 2.5 cm × 0.3 cm plexiglass rectangles on top of polystyrene vials 5.5 cm high and 2.5 cm in diameter (Figure 1). This arena setup is the same as has been used in other studies on bumblebee cognition (Jones et al. 2023; Jones and Agrawal 2016; Dawson et al. 2013; Richman et al. 2021; Wolf and Chittka 2016). Colonies of *Bombus impatiens* were purchased from Koppert (Koppert Biological Systems, Howell MI USA). One colony was attached to each arena and bees were provided access to the arena via a clear tube with sliding plexiglass doors. Six different colonies were used with each colony undergoing a 5–10 day training period. During this training period the entire colony was given access to the arena and allowed to forage on colorless transparent flowers with large

(~1 mL) drops of 0.7 M sucrose solution. Any bees seen foraging at flowers were captured, tagged on the thorax with a colored numbered bee tag, and released back into the arena.

Following the training period, individual bees were tested in the same arena with an alternating pattern of 6 blue (Perspex Blue 727) and 6 yellow (Perspex Yellow 2252) artificial flower squares. A reward of 5 µL of 0.7 M sucrose solution was provided on each flower at the start of every bout and was refilled when consumed by the bee. Each foraging bout ended either when the bee returned to the colony on its own or after 5 min passed with no visit (at which point the bee was captured and returned to the colony). The next bout began when the bee left the colony and entered the entrance tube. Every bee performed three consecutive foraging bouts, with all bouts occurring on the same day. Every bee was allowed 3 foraging bouts and we videorecorded the bouts with a GoPro HERO7 at 30 fps. For the sake of keeping extraneous variables constant the lighting in the arena was kept consistent. Additionally, our data analysis required the GoPro to remain in a consistent position relative to the flower array, but changing either the lighting or the camera position should not have had a significantly adverse effect on the DeepLabCut network performance. We analyzed data from a total of 13 bees (1–3 from each of the 6 colonies) that completed all three bouts (39 total trials).

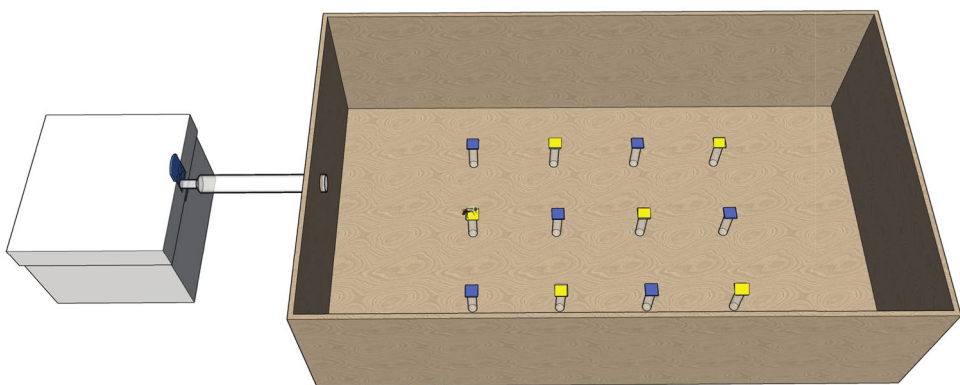


Figure 1. Experimental setup in which a colony of bumblebees are attached via a plexiglass tube to a foraging arena with 12 artificial flowers. Figure to scale.

Analysis was performed using DeepLabCut, an open-source pose estimation software (Mathis et al. 2018; Nath et al. 2019). We extracted 667 frames from the GoPro videos, labelled them, and used them to train the neural networks. The neural networks were tasked with identifying only two points: the bee and a marker indicating the entrance of the bee's colony. The entrance marker was included because we used two arenas with opposite entrance positions relative to the camera angle and tagging the entrance to the colony made for easier downstream analysis. A frame from each of the 39 videos was additionally extracted and the positions of three flowers marked. As neither the flowers nor the camera moved during a bout, a single frame of reference was adequate for determining the flower's positions throughout the bout. The neural networks were then used to analyze all 39 videos. The output from DeepLabCut and the reference points were fused to determine the bee's location relative to the flower array for every frame using R (version 4.1.3). A visit was defined as any time when the bee point was within a 40×40 pixel

square centered on the flower. Visits less than 1.5 s long were disregarded, due to the tendency of bees to hover near a flower, fly over flowers, or land briefly on flowers without drinking. To minimize the impact of a DeepLabCut labelling error, any flight shorter than 1.5 s that occurred between visits to the same flower was disregarded and added to the visit time.

Using the lme4 (Bates et al. 2015) and car (Fox and Weisberg 2018) packages in R we analyzed factors influencing the number of visits to each flower in the arena. We used a linear mixed effect model of the number of visits bees made to each flower in the arena with fixed effects of the bee's experience with the flower within that bout (a binomial variable of previously visited or not) and the flower color. Both bee and colony were included as random effects. We then analyzed the duration of each flower visit using a linear mixed effect model with fixed effects of the foraging bout number, whether the bee had visited that flower before in that bout, and the flower color. This model also had individual bee identity and colony as random effects. We created a

Examples of Typical Frames Labelled by DeepLabCut

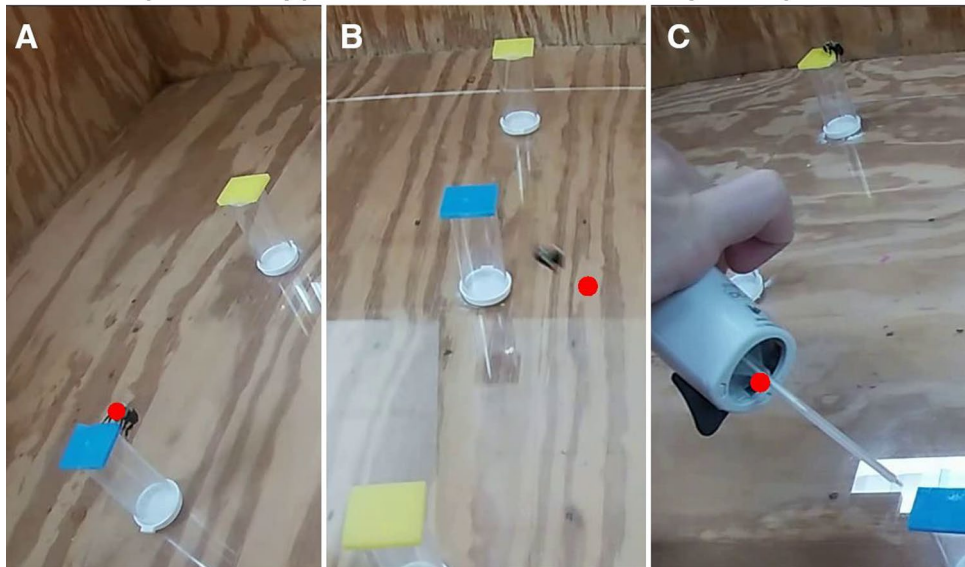


Figure 2. Representative examples of frames labelled by DeepLabCut. **A** Correctly labelled frame. **B** Misplaced label during bee flight. Fast moving bees combined with low framerate cause these errors. The network still correctly identifies the bee as moving and off a flower, however these errors reduce path analysis accuracy. **C** Misidentification of a bee during a visit. Such an error can contribute to the network returning a false duration or completely missing a visit.

third linear mixed effect model to assess the percentage of time bees spent on flowers versus in flight with foraging bout as the fixed effect and bee and colony as random effects. Percentage of bout time spent on flowers was chosen as a metric of foraging efficiency, as bees who spend more time flying and less time visiting flowers are using energy less efficiently. We conducted posthoc comparisons between bouts on this last

model using the emmeans package (Lenth et al. 2022) with Tukey-adjusted P values.

3. RESULTS

3.1. Accuracy of DeepLabCut analysis

Of the frames autonomously labelled by the DeepLacCut network, 4,481 frames were checked

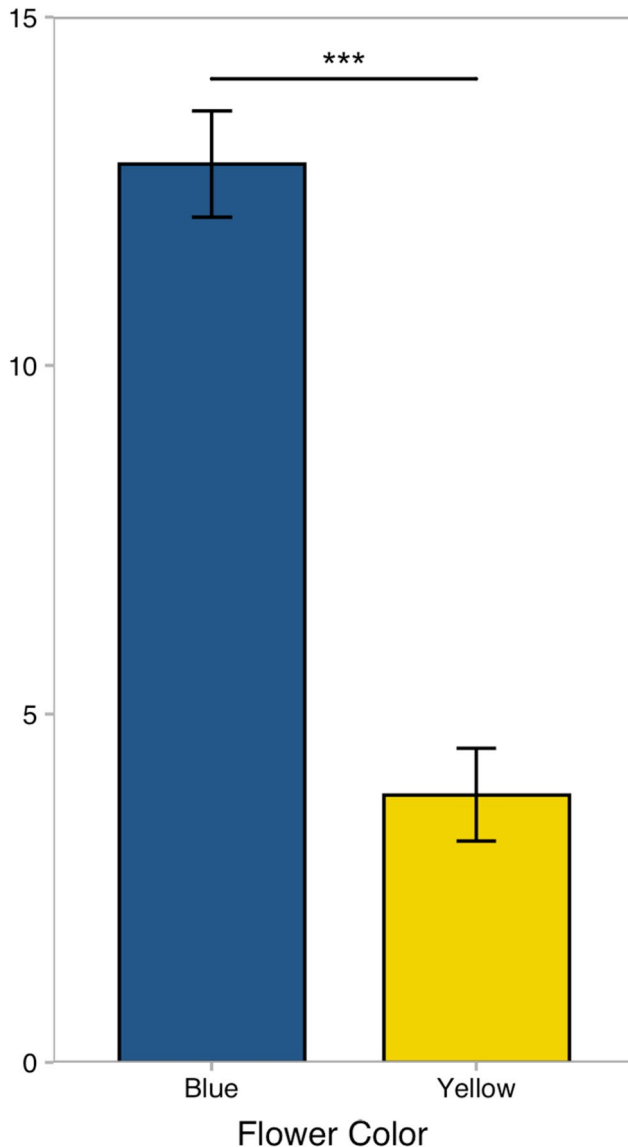


Figure 3. Flower color influenced bee visitation rates, with bees greatly preferring blue flowers over yellow flowers. Error bars represent standard error of the mean.

for correct labelling, and 123 were identified as mislabeled, an accuracy rate of 97.3%. Of the mislabeled frames: 101 (82.1%) captured the bee in flight and 13 (10.6%) mislabeled a background element as the bee when the bee was not visible to the camera. Only 5 (4.1%) of the mislabeled frames were a result of the network labelling something besides the bee while the bee was making a visit, making the overall accuracy for labelling visiting bees 99.9% (Figure 2).

3.2. Bumblebee behavior

Flower visitation was affected primarily by flower color with more than three times as many visits to blue flowers than yellow flowers ($\chi^2=80.159$, $df=1$, $P<0.001$; Figure 3). Within a single bout, visit duration was affected by previous visit with 19.5% shorter visits to previously visited flowers ($\chi^2=9.823$, $df=1$, $P=0.002$, Figure 4), and no effect of color. Across all three bouts visit durations

got shorter, with post-hoc comparisons demonstrating that the visit duration to flowers was shorter in the third bout than the first bout ($\tau=3.771$, $df=108$, $P<0.001$, Figure 5). Bee foraging became more efficient over the three bouts, with bees spending a higher percentage of their third bout on flowers than in flight when compared to their first bout (LMM; $\chi^2=6.119$, $df=2$, $P=0.0469$; Figure 6). Arena identity had no effect on bee behavior.

4. DISCUSSION

We have demonstrated the use of DeepLabCut in tracking individual bees over an entire foraging bout and shown that foraging efficiency increases with experience, measured by a decrease in proportion of time spent flying versus foraging. This result is congruent with previous studies showing that bees forage more efficiently in terms of a decrease in

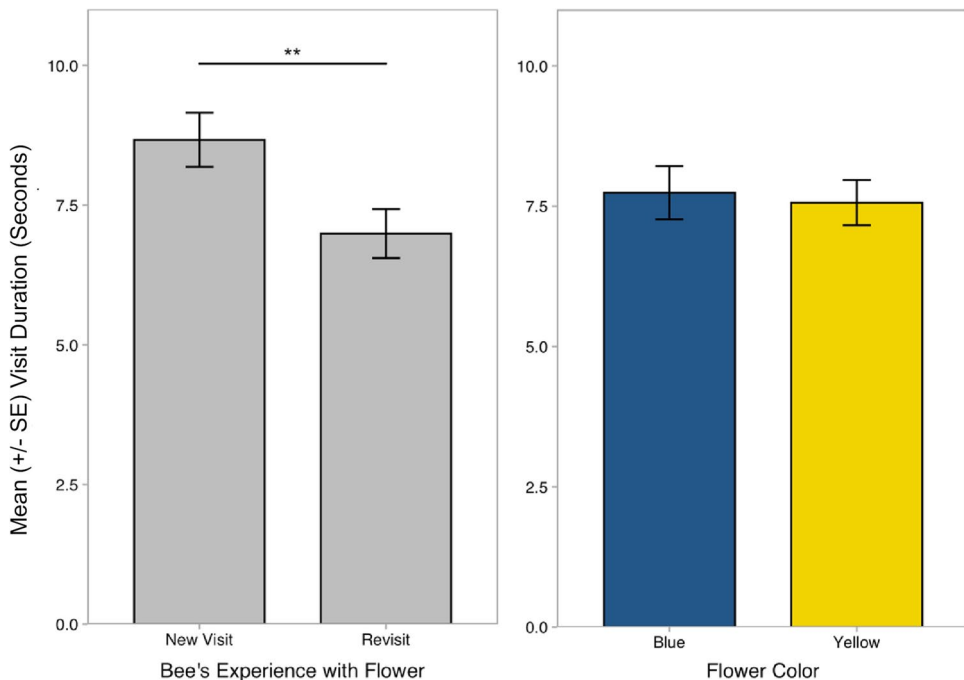


Figure 4. Visit duration is only affected by experience, and not an overall function of flower preference. Average duration of visit was significantly lower during revisits, potentially signifying the role experience plays in investigating and feeding on a flower. Despite playing a large role in flower preference, flower color demonstrated no effect on visit duration.

flight lengths and foraging bout durations with increased foraging experience (Klein et al. 2019; Woodgate et al. 2017). We additionally found that bee visits to flowers were shorter across foraging bouts and visits to specific flowers were shorter when they were revisits within a foraging bout, despite nectar supply having been refilled. This result confirms previous work on visit duration, where bee experience with complex artificial flowers was negatively correlated with visit duration (Lavery 1994; Leonard and Papaj 2011). Other studies have shown that experience is only one factor influencing visit duration, as floral pattern and olfactory cues can assist in nectar discovery and thus shorten visit duration (Lawson et al. 2017; Leonard and Papaj 2011). Visit duration has been shown to affect pollination success (Kendall et al. 2022; Jones et al. 1998), therefore any factor that impacts a bee's visit duration may be important for plant fitness. In the context of bumblebee research, the duration of individual visits to flowers is often an unstudied metric of bee foraging optimization, owing to the difficulty of measurement during free-flying assays. Our data shows that visit duration, in the absence of pollen collection, floral patterning, or olfactory cues, is directly affected by experience, indicating it may be a useful metric through which to study bee foraging efficiency.

DeepLabCut is well suited to a variety of future applications, especially considering the ease of its use and implementation. It enabled the measurement of visit duration and thereby foraging efficiency in our study, in a lab not designed for motion tracking experiments, and with researchers lacking computational expertise. The addition of DeepLabCut to our lab's existing protocols, the analysis of each video, and the subsequent data analysis was all accomplished by researchers with no previous coding experience. The code developed for the data analysis in our study has been posted to Github (<https://github.com/JonesLabBowdoin/Markerless-Tracking-of-Bumblebee-Foraging-Allows-for-New-Metrics-of-Bee-Behavior>) to further facilitate DLC implementation in other labs. Moreover, the trained neural networks produced by this experiment

can be applied to any number of future experiments using the same arenas, allowing for very fast future analyses. Additionally, DeepLabCut has further applications to free-flying foraging not covered in this study, such as measuring path length, flight speed, flower approach direction, and body angle. Other utilities might include tracking on complex backgrounds and tracking multiple body parts to record behaviors such as antennation or grooming after flower visits.

In future applications of DeepLabCut to free flying foraging experiments, accuracy can be increased in a few simple ways. The simplest would be to use a camera with a higher framerate. A low framerate and a fast-moving bee can lead to both blur and large positional "jumps" between frames, both of which are difficult for DeepLabCut to interpret. Additionally, the number of times the software misidentifies a non-bee object for the bee can be diminished in the future by having a camera which covers more of the arena, and by avoiding the number of moving objects within the frame (e.g., not refilling

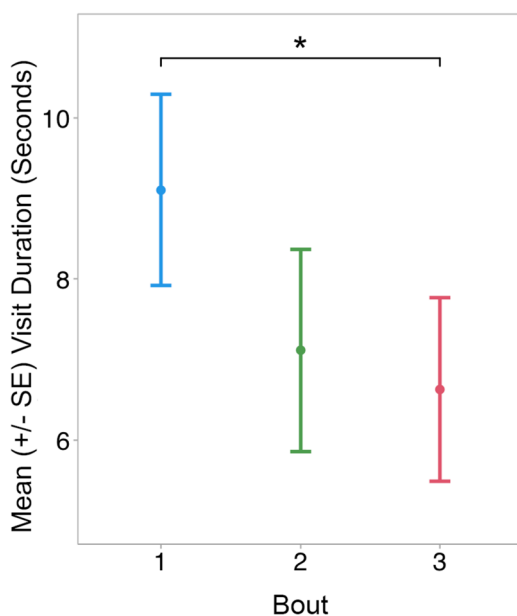


Figure 5. Mean visit durations for the bumblebees' three foraging bouts. Visit durations in the third bout were significantly shorter than the visit durations in the first bout. Error bars represent standard error of the mean.

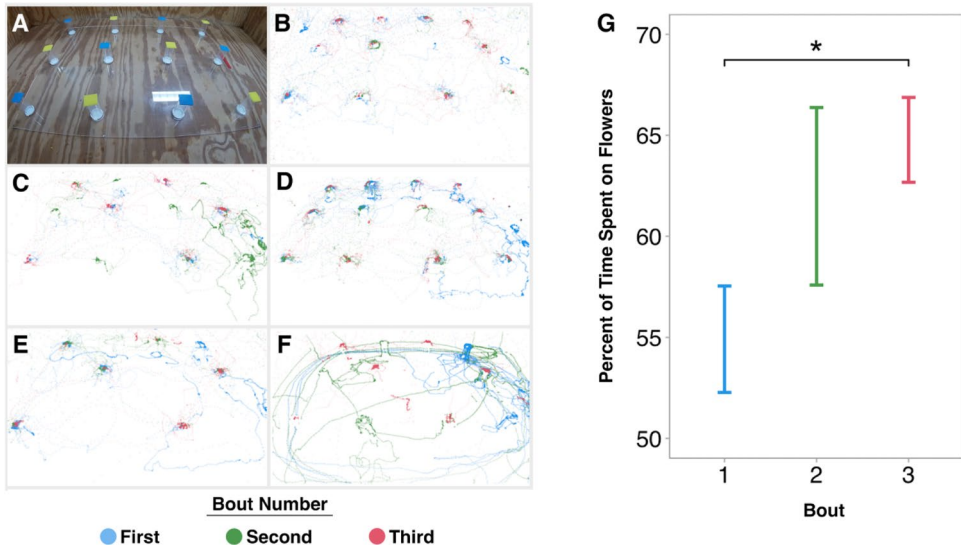


Figure 6. A view of arena from video used in analyses. **A–F** Trajectories of 5 individual bees engaging in 3 bouts each. Plotted from the raw x and y coordinates outputted by DeepLabCut. **G** The mean and standard error of foraging efficiency, i.e., the percent of time bees spent on flowers versus not visiting flowers, over all three foraging bouts. Asterisk indicates significant differences between bouts 1 in and 3.

flowers during a bout or using automatically refilling flowers). In our experiment, we used flat plastic squares as flowers, which allowed the bumblebees great freedom in how they moved and posed while drinking the nectar solution. Artificial flowers that have only one opening through which to access nectar will lower the number of poses a bumblebee can exhibit while visiting and increase the accuracy of labelling.

As DeepLabCut and other tracking algorithms become more popular in behavioral ecology, they will enable researchers to ask novel questions that rely on precise quantification of behavior through tracking multiple moving points in video analysis. In this simple experiment, DeepLabCut allowed us to easily measure metrics of bee foraging behavior without substantially changing our experimental design. The quantification of visit duration and its connection to bees' previous experience additionally gives future researchers more tools with which to study bumblebee behavior.

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AUTHORS CONTRIBUTION

PLJ conceived of the experiment and both PLJ and RW contributed to the experimental design. Both authors contributed to data collection and analysis. RW wrote all original code and first draft of the manuscript. Both authors commented on subsequent versions of the manuscript. Both authors read and approved the final manuscript.

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DATA AVAILABILITY

Data is available at <https://github.com/JonesLabBowdoin/Markerless-Tracking-of-Bumblebee-Foraging-Allows-for-New-Metrics-of-Bee-Behavior>.

CODE AVAILABILITY

Source code available at <https://github.com/JonesLabBowdoin/Markerless-Tracking-of-Bumblebee-Foraging-Allows-for-New-Metrics-of-Bee-Behavior>.

DECLARATIONS

Ethics approval Not applicable.

Consent to participant Not applicable.

Consent for publication Not applicable.

Conflicts of interest Financial Interests: Reed Warburton and Dr. Jones declare they have no financial interest.

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