

Disruption in honey bee (*Apis mellifera*) foraging flight activity during a partial solar eclipse shown by individual flight path tracking

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Abstract

Honey bee (*Apis mellifera* L.) foraging activity is dependent on solar and celestial cues. To better understand how bee flight activity is influenced during a solar eclipse, individual departing and returning flights were quantitatively analyzed using a video-based tracking tool during a partial solar eclipse on 23 October 2014 in Woodside, California. Compared to a control (non-eclipse) day, there was a significant overall increase in foraging flight activity of 15% (1.16 vs. 1.01 baseline for day 1 and 2, respectively) at maximal solar obscuration (39%). Both departing and returning flights showed increased occurrence corresponding to the eclipse peak, followed by a gradual restoration of normal activity during eclipse resolution. Instantaneous flight activity was correlated ($r = -0.63$) with changes in global horizontal irradiance during the eclipse. These data provide greater insight into how subtle changes in skylight properties modulate foraging flight behaviour.

Key words: eclipse, honey bee, flight analysis, foraging.

Introduction

Flight activity and, by extension, foraging by members of the genus *Apis* is governed by a number of integrated environmental cues, with time, light, and temperature being the most critical determinants (Moore *et al.*, 1989; Vicens and Bosch, 2000; Woyke *et al.*, 2003; Pahl *et al.*, 2007). Visual cues from the sky and the pattern of polarized light enable foraging bees to successfully navigate to sources of food and nectar, and then to complete the return trip back to the hive (van der Glas, 1980; Rossel and Webner, 1984).

In *Paradise Lost*, John Milton described the terror and thrill of an eclipse to both humans and insects: “*As when the Sun, new risen, ... / in dim eclipse, disastrous twilight sheds / On half the nations and with fear of change / Perplexes monarchs.*” Because of their reliance on environmental inputs for foraging and lifecycle decisions, insects are exquisitely sensitive to subtle changes in light conditions. The behaviour of bees during solar eclipse conditions has been described utilizing direct observation and semi-quantitative methodology (Lundie, 1940; Woyke, 1954; Roonwal, 1957; Nakano, 1958; Holmes, 1963; Nitschann 1999; Showler, 1999; Pechhacker, 1999; Woyke *et al.*, 2000).

Independent of percent solar obscuration, the majority of prior reports describe an overall increase in bee flight activity at the hive entrance corresponding to the time of maximum eclipse (Woyke, 1954; Roonwal, 1957; Woyke *et al.*, 2000). Interestingly, the magnitude of change in observed flight activity is hypothesized to be determined not by the percent of sun coverage, but by the direction of increases or decreases in solar irradiance during the eclipse (Woyke 1954; Gedzelman, 1975; Fernandez *et al.*, 1993; Woyke *et al.*, 2000; Kopke *et al.*, 2001). To better understand the effects of rapid changes

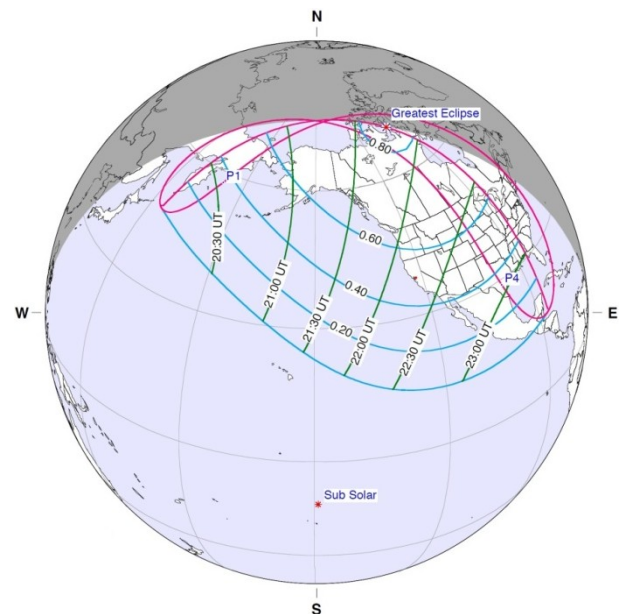


Figure 1. Partial solar eclipse of 23 Oct 2014 (Esenak, 2014). Maximum solar obscuration at our apiary (indicated by a red dot) occurred at 15:17 local time. (In colour at www.bulletinofinsectology.org)

in solar irradiance, we utilized bee flight tracking software to analyze the flight behaviour of a bee colony during a partial solar eclipse.

Materials and methods

Solar eclipse and astronomical data

On 23 October, 2014, a partial solar eclipse occurred over Northern California (figure 1) with a maximum obscuration of 39% (Esenak, 2014). Changes in solar

irradiance were calculated based on relative sun and moon positions at our GPS location (37°26'27.2"N 122°15'54.8"W) using NREL's Solar and Moon Position Algorithm (Bird and Hulstrom, 1981) assuming standard atmospheric conditions for the following scenarios: 1) global horizontal irradiance (GHI), defined as the total amount of shortwave radiation received from above by a horizontal surface, including both direct normal irradiance (DNI) and diffuse horizontal irradiance, the from sun's unshaded lune, and 2) DNI, defined as the amount of solar radiation received per unit area by a surface held perpendicular to the sun's rays at its current position in the sky.

Video collection and activity processing

The colony consisted of 1 deep brood box with an entrance reducer (9 cm opening), and was inspected 1 week prior to ensure it was queen right and robust. Food stores were sufficient for colony size (2 frames of honey, 2 frames mix of honey and pollen, and 6 frames mix of sealed brood, open brood, and pollen). The hive had sufficient room to increase both food storage and brood area and was not in season or condition for swarming. The hive was separated from nearby hives by 3-5 meters in all directions to minimize cross-flights and/or other confounding sources of movement.

Bee flights were digitally recorded on 23 October 2014 during a partial solar eclipse, and the following control day, 24 October 2014, in Woodside, CA in an open apiary. On recording days, at 15 min intervals from 13:45-16:45 Pacific Daylight Time, 2 minutes of digital video was acquired using a tripod-mounted Sony HDRCX130 video camera with optical stabilization at 1920 × 1080 resolution at 29 frames per second and stored card. Raw video was decoded to individual loss-less PNG format image frames using ffmpeg (<http://ffmpeg.org/>; ver. N-60859-g313a6c6) in 30 second intervals at 960 × 540 resolution on an Intel 3.30 GHz computer running MS Windows 7.

Individual frames were analyzed with the *tracks.py* (Goddard, 2011) software written in Python (ver. 2.7) using the Python Image Library (ver. 1.1.7), and NumPy scientific computing module (ver. 1.8.0). *Tracks.py* computes an average static image which represents the background of the video, then compares each video frame to the average to detect differences which represent flying bees. The software identifies bees by detecting pixel positions in frames that differ from the average by a threshold variation of 10 ($r \times r + g \times g + b \times b$, where r, g, b, are colour differences), and pixel spacing between detected maxima in difference images (set to 12 pixels). The program rejects a connection if the apparent motion is > 4 times the motion from a previous frame. If the target bee is not found in a subsequent frame, the software looks ahead another frame to account for background blending.

Flight paths of individual bees are identified by tracking pixel differences in sequences of video image frames, which are superimposed onto the static background image. Paths are extended forwards and backwards in time. An individual bee position can only be used in one path. The program identifies and displays

accelerating (increasing flight speed) and decelerating (decreasing flight speed) flight paths of bees. This program enabled us to quantify flight activity and to determine if bees were returning or departing from the hive. Reassembly of image frames into a tracked video was performed using ffmpeg (h264 mp4 format, 960 × 540 resolution at 42 fps).

Image analysis

To eliminate the influence of movement artifact from trees, etc., flight activity was quantified with a 3 × 3' region of interest (ROI) centered on the hive entrance using ImageJ (ver. 1.49i; Rasband, 1997) image analysis software. The ROI was mapped to 30 sec of superimposed flight activity on an individual image at each recording timepoint. Images were thresholded and analyzed using the particle analysis module (pixel size 0-infinity, circularity: 0.00-1.00) to determine overall flight activity per total frame area. Plots were generated for total flight activity, decelerating flights, and accelerating flights on each day, and graphed individually or in composite for each 30 sec recording period as tracks per interval. The rectified difference in total activity was calculated.

Statistical analysis

All data were checked for normality using the Shapiro-Wilk test. Differences in between-group measures were evaluated using the non-parametric Wilcoxon rank sum test, with significance set at < 0.05. Pearson product-moment correlation coefficient was used to evaluate the relationship (*r*) between change in flight activity between days 1 (23 October 2014) and 2 (24 October 2014), and solar irradiance. Linear regression was used to establish a separate relationship between flight activity and GHI. Statistical analysis was performed using SigmaPlot version 12.1 (Systat Inc., San Jose, CA).

Results

Eclipse and meteorological conditions

At the site of video collection, the eclipse (figure 2) penumbra began at 13:53 Pacific Daylight Time at a direction of 199° at an altitude of 38.6°, was maximal at 15:17 (222°, 30.7°), and ended at 16:33 (238°, 18.7°). Maximum obscuration of solar disk was 39%. During the 3 hour recording period on 23 October 2014, the temperature ranged from 20-23 °C, atmospheric pressure was 1015-1018 hPa, and there was a light Northwesterly 6-12 kph wind. On 24 October, recording conditions were similar at 21-23 °C, 1012-1014 hPa, and a 6-11 kph wind from North, with no cloud cover.

Solar irradiance

The area of unshaded solar lune was calculated for 23 and 24 October, 2014 around the flight activity recording period from 12:00-18:00. The total obscuration was determined to be 39% at our apiary location, with eclipse onset, peak, and end corresponding to predicted times (figure 2). At eclipse onset on day 1, the GHI was

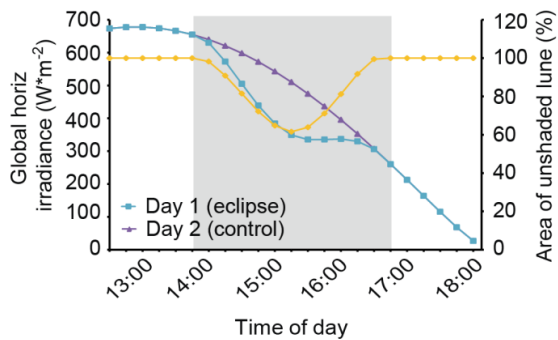


Figure 2. Computed global horizontal solar irradiance from 12:30-18:00 during day 1 (23 October 2014) (eclipse, blue line) and day 2 (24 October 2014) (control, purple line). Area of unshaded lune (exposed sun) is indicated by the yellow line. The gray area indicates when video recordings and analysis were performed. (In colour at www.bulletinofinsectology.org)

calculated to be 630 W/m^2 , which decreased to 349 W/m^2 at maximal obscuration. During the second half of the eclipse GHI decreased further to 335 W/m^2 before rising to 337 W/m^2 as the eclipse ended. On day 2, un-

der the same atmospheric conditions, the GHI peaked at 678 W/m^2 at 12:45 hr and then decreased through the rest of the afternoon. DNI was transiently reduced in a similar manner during the eclipse, however there was greater recovery during the second half of the eclipse (to % normal levels relatively sooner than GHI).

Flight tracking

Individual honey bee flight paths identified from a 30 second video clip superimposed on an averaged background image are shown in figure 3. Accelerating (green) and decelerating (red) flights are represented. Tracks may have abrupt initiation and termination points due to perpendicular or oblique flight paths and/or flights that move out or into the range of detection ($\sim 10 \text{ m}$). Tracks showed characteristic flight features of putative departing and returning foragers whereby arriving bees had gradually more variable paths as they approached the hive landing board. In contrast, departing bees had more direct paths as they left the hive entrance. Normal landing board activity observed (nectar exchange by nurse bees, cleaning, et cetera) which led to introduction of noise (yellow) in the composite image.

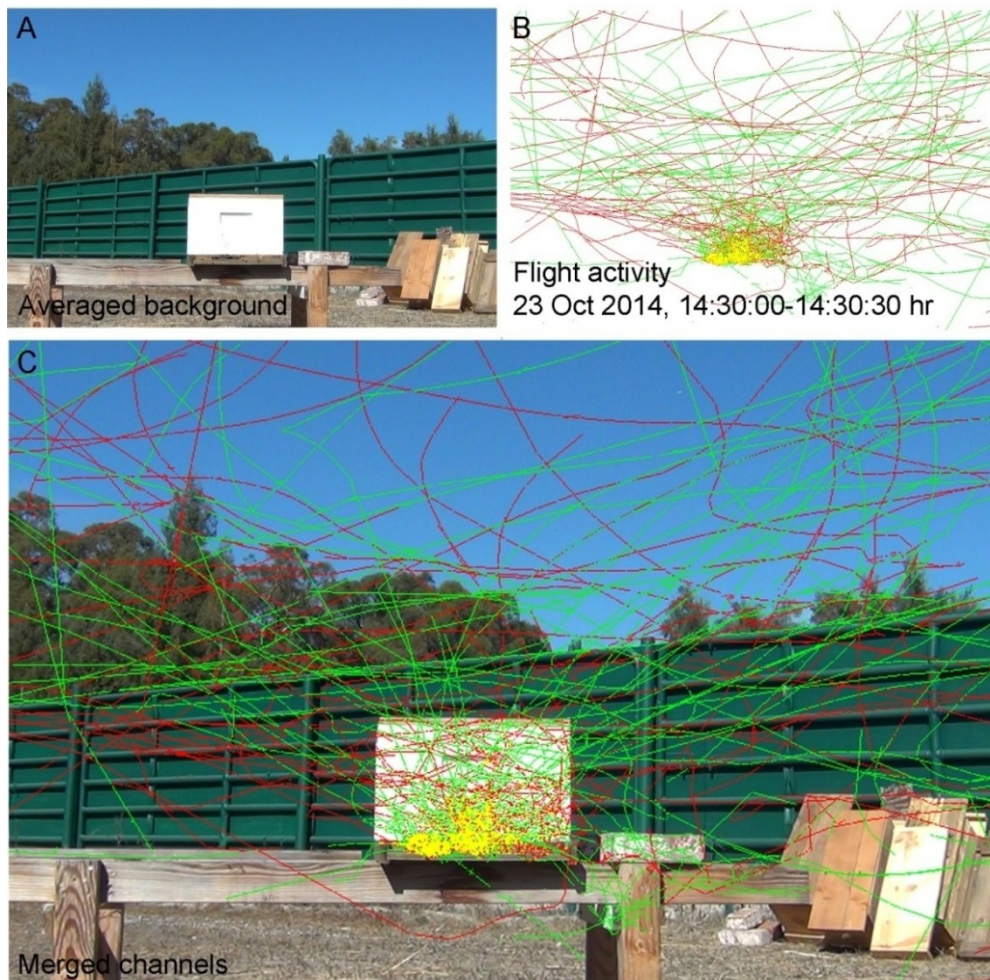


Figure 3. (A) Target hive setup and averaged background image. (B) Representative flight tracks recorded over a 30 second interval are shown. Green and red lines indicate putative accelerating and decelerating individual flight paths. Yellow regions show green-red channel merge. (C) Flight activity superimposed over the background image. (In colour at www.bulletinofinsectology.org)

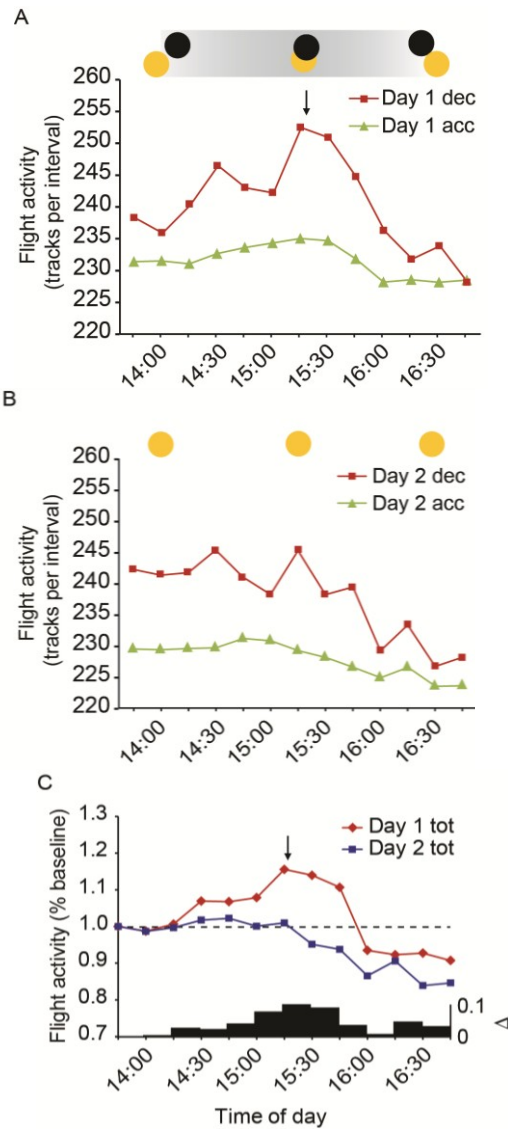


Figure 4. Normalized flight activity during (A) day 1 (23 October 2014) and (B) day 2 (24 October 2014) quantified over 30 second intervals at time points indicated. Total flight activity is shown in blue, decelerating flights in red, and accelerating flights in green. Solar obscuration is represented graphically for each day. (C) Total normalized flight activity on days 1 and 2 showing difference at each time point; black bars are difference values, arrow indicates peak eclipse point at 15:17. (In colour at www.bulletinofinsectology.org)

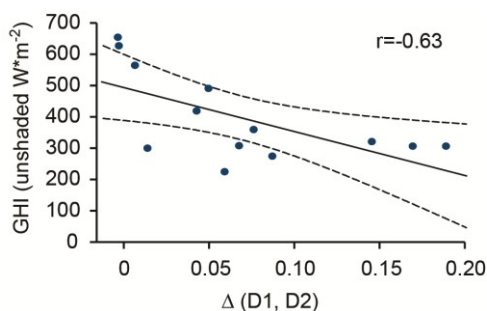


Figure 5. Correlation of global horizontal irradiance (GHI) and difference in flight activity on day 1. Dotted lines indicate 95% confidence interval.

Quantitative analysis of flight track activity (figure 4) showed differences between days 1 and 2. Although pre-eclipse flight activity was equivalent (238 and 243 tracks per interval for decelerating flights, and 231 and 230 tracks per interval for accelerating flights, on days 1 and 2, respectively), on day 1 (figure 4A), decelerating bees demonstrated a significant ($p < 0.001$) increase in flight activity. The peak difference corresponded to the maximal obscuration of the eclipse (252 tracks per interval), followed by a gradual decrease in activity on both days and convergence by 17:00 hr. Acceleration flights showed a transient increase corresponding to the peak eclipse (234 tracks per interval), with an overall trend of decreased activity over the course of recordings. In contrast, on day 2 (figure 4B) decelerating and accelerating flights showed a net decrease in activity over the course of the recording period, with only transient increases and decreases detected in the deceleration and acceleration.

The difference in total flight activity between days 1 and 2 is shown in figure 4C. Flight activity on each day was normalized to the 13:45 hr timepoint. Total flights on day 1 showed a net increase starting at the onset of the eclipse, with a peak occurring just before maximal obscuration of 15:15 hr (15% vs. day 2 at this timepoint; 1.16 vs. 1.01, respectively). At the last timepoint analyzed (16:45 hr), the difference in total activity was 7% (0.91 vs. 0.84 baseline for day 1 and 2, respectively). In contrast, on day 2 net flight activity decreased starting at around 15:15 hr. The difference in total flight activity between days 1 and 2 was calculated and shown as a histogram in panel C, which is significant ($p = 0.027$).

Correlation of flight activity with solar irradiance

Instantaneous flight activity from 13:45-16:15 hr was negatively correlated with GHI from the sun's unshaded lobe ($r = -0.63$, $p = 0.02$; figure 5). When total flight activity was compared with unshaded DNI, the correlation coefficient was stronger ($r = -0.83$).

Discussion

Our data demonstrate that 39% solar obscuration causes changes in bee flight activity. Bees forage at temperatures above 12-19 °C and solar irradiance greater than 400 W/m² (Heinrich, 1979; Burrill and Dietz, 1981; Vicens and Bosch, 2000). Apiary temperatures did not decrease below 20 °C during the eclipse, therefore body temperature was not a likely contributor to changes in flight activity. Given eclipse-induced changes in GHI, skylight characteristics were likely a key factor in influencing observed flight activity. During the eclipse, at maximal obscuration, GHI dropped 31% to 349 W/m² from 510 W/m² predicted on a normal day at the same time. Modeling of solar irradiance showed a stronger correlation with DNI ($r = -0.83$) than GHI ($r = -0.63$) suggests that direct sunlight was more influential than scattered rays.

Compared to the non-eclipse day, we observed an immediate divergence in total flight activity starting at the eclipse onset. Whereas on day 2 flights showed a gradual

decrease coincident with time of day (mid-late afternoon), on day 1 total flight activity increased leading up to maximum solar obscuration, and then decreased after this time to eventually converge with that observed on day 2. Considering differences in time of day, our results are consistent with Woyke *et al.* (2000) who showed that during an eclipse of 86% obscuration in Warsaw at 12:51 hr, more forager bees returned to the hives before maximum obscuration in increased number, and left in relatively lower numbers with the progress of the eclipse. During an eclipse of 95% obscuration, the largest number of foragers returned to the hive 10-20 min before the peak eclipse (Woyke, 1954). These results indicate that bees are highly sensitive to light intensity levels (Labhart, 1974), and that the determining factor in foraging flight activity is not percentage of sun coverage, but direction of increasing or decreasing solar obscuration (Woyke *et al.*, 2000).

Bees are central place foragers that navigate back to their nests after food searching excursions. It is well known that the Sun is used as a reference in the bee's internal compass for such navigation (Lindauer, 1960; von Frisch, 1993). Behavioural experiments have not only shown that the position of the sun plays an important role in sky compass orientation but also polarization pattern of the sky and chromatic intensity gradients can also be used as navigational cues (Brines and Gould, 1982). In addition to information in the sky, salient landmarks that the bees may experience during route training between hive and food source can override the sun compass and guide bees in direct flights to the hive (Cheeseman *et al.*, 2014). However, bees possess a backup navigation system for cloudy days and are able to navigate to familial food sources and communicate by determining solar azimuth through a memory of the sun's course with respect to local landmarks (Dyer and Gould, 1981; Dovey *et al.*, 2013).

Light scattering in the atmosphere creates a chromatic gradient that varies in intensity and forms a pattern of polarization with tangential electric field vectors arranged along concentric circles around the sun (el Jundi *et al.*, 2014). When the sun is blocked by a cloud, bees are able to obtain a compass reference from the unobscured part of the sky by making use of this pattern of polarization (Wehner, 1989). This polarization-analyzing system can be 'switched on' during flight only when the bee experiences a polarized-light pattern in the dorsal region of its visual field (Wehner and Labhart, 2006).

When bees have clear readings of the sun or polarized light patterns from the sun, successful navigation occurs. However, variations in the angle and degree of skylight polarization from eclipse events (Shaw, 1975; Horváth *et al.*, 1999; Pomozi *et al.*, 2001; Sipócz *et al.*, 2008) may alter navigational and foraging patterns. The mechanistic reasons for increases in returns and/or departures from colonies during an eclipse have not been suggested or determined, and we speculate that increases in flight activity could be caused by a number of factors: 1) field foraging bees sense deviations from internally-anticipated relationships between solar irradiance, time-linked azimuth, and celestial and astronomical cues during an eclipse (Dyer and Dickinson, 1994; Towne and

Moscip, 2008) and react by returning to the colony; 2) bees departing from the hive have difficulty reading sun and polarization features of the sky and return quickly; and/or 3) bees that return quickly after a failed foraging trip attempt subsequent (unsuccessful) trips.

The total flights observed on day 1 showed a net increase starting at the onset of the eclipse, with a peak occurring just before maximal obscuration (15% vs. day 2 at this timepoint). These findings of increased return rate could be additive from bees returning from regular foraging trips combined with bees returning from failed attempts at departure. Woyke *et al.* (2000) found that foragers did not stop to leave the hives at 86% obscuration, rather they left the hive in high percentage. In our study we noticed slight increases in departure rates as well. These additional departures could be the addition of one cohort of regularly departing bees with a cohort of bees making a second attempt from prior navigational setbacks. In Woyke *et al.* (2000) and our study, the number of foragers returning to hives continued to decrease after maximum obscuration and we believe this is because navigational perception improves success of foraging flights and the bees presumably remained in field.

There are a number of caveats to be considered regarding our flight tracking methodology. To identify individual bee flight tracks, *tracks.py* computes an average image which represents the static background of the video, then compares each video frame to identify differences more than a specified threshold value (flying bees). Maxima in consecutive frames and close in space are then joined to form a path. The average image uses a moving window consisting of 30 frames before and 30 frames after the analyzed image frame. Despite these error correction features, there is currently no code that rejects motion generated by non-bee objects. Though we attempted to eliminate all sources of possible noise by removing brush and weeds from the ROI, it is possible that background movements may have been classified as flight movements. Additionally, non-flight locomotor activity on hive landing boards produced flight signal artifact, and for this reason all quantitative analysis excluded these regions of video. Inter-frame tracking is performed by locating a bee's position in one frame and comparing it with the nearest bee position in the subsequent frame, and rejecting motions from one frame to the next greater than 4 times the motion for that bee in the previous frame. To account for cases where a bee was not detected in a frame most likely because it was against a similar colour background, the program looks ahead one more frame. This can produce loss of tracking artifacts, which could be incorporated into the quantitative assessment.

Finally, it is possible that inter- and intra-day nectar and/or pollen sources or quality, or the food demand within the colony, could have changed from day 1 to day 2, and influenced flight activity. While we didn't directly measure the incoming nectar/pollen levels, we noted that on both days the bees were flying in same direction possibly to same floral source that has the same daily pattern of nectar production when temperature, sun intensity etc. are similar as they were on both days. Qualitatively, the pollen colour was similar for both days.

Conclusions

At the individual level, systems such as radio frequency ID tags (RFIDs) could be used to better understand the cohort of returning bees during the time of maximum eclipse and help determine from what distances and under what navigational conditions they may have returned. It will be important in future work to investigate in greater detail the interplay and between solar irradiance and ephemeris, quality of forage, hive demand, and other environmental factors in honeybee foraging.

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