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Tracking individual *Bactrocera tryoni*: Wind effects and natural movement

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Abstract

Determining the movement characteristics under real-world conditions of insect pests, such as tephritid fruit flies, is critical to increase the effectiveness of detection, response, and control strategies. In this study, we conducted two experiments using harmonic radar to track wild-caught male Queensland fruit flies (Qflies), *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae), a major horticultural pest in Australia. In Experiment 1, we continuously tracked individual Qflies, which were prodded to induce movement in a high-density papaya (*Carica papaya*, L., Caricaceae) field. We conducted Experiment 2 in a field with lower papaya density and tracked flies were allowed to move without disturbance. This latter natural movement experiment showed that Qflies move at a rate of (mean ± SE) $19 \pm 3\,m\,h^{-1}$. In both experiments, overall and between-tree flight directions were found to be correlated with wind direction, whereas within-tree movement directions were not. Further, the effect of wind direction on fly trajectories varied by step distance but not strongly with wind speed, whereas step-distance distributions were consistent with Lévy walks (i.e., short random steps with occasional larger steps). Qfly movements were well fitted by two-state hidden Markov models, further supporting the observation that Qflies move differently within (short steps with random direction) and between (longer more directional steps) trees. Data on flight directionality, step distances, and movement speed determined in this study provide parameters that may help enhance current surveillance, control, and eradication methods, such as optimizing trap placements and pesticide applications, determining release sites for parasitoids, and setting quarantine boundaries after incursions.

KEYWORDS
Diptera, directional movement, dispersion, field tracking, harmonic radar, movement rate, step distance, Tephritidae, turning angle, wind

INTRODUCTION

Characterizing the natural movement parameters of insect pests is critical to improving our responses to them. This includes developing realistic models to increase the effectiveness of control and surveillance strategies, assessing maximum movement probabilities, and setting thresholds for areas under treatment. Parameters of particular importance for models of insect movement include step distances, turning angles, and speed. For the Queensland fruit fly (Qfly), *Bactrocera tryoni* (Froggatt) (Diptera, Tephritidae), and other tephritid fruit flies, mark–release–recapture (Sonleitner & Bateman, 1963),

flight mills (Chapman, 1982), and visual observations have been used to determine movement behaviors. However, none of these techniques give a complete picture of movement under real-world conditions. Tracking tagged individual flies (Miller et al., 2022) offers an alternative method to determine natural movement parameters, which mirrors well-established studies conducted by ecologists on larger animals (Lennox et al., 2016).

Relatively few dipteran spp. have been studied using tracking devices (Batsleer et al., 2020) as flies are generally small- to medium-sized; therefore, requiring small, light tags. To our awareness, all dipteran tracking studies have utilized harmonic radar (HR) (Chapman et al., 2004; Roland et al., 1996) with studies on tephritids including research on *Bactrocera minax* (Gui et al., 2011; He et al., 2019; Huang et al., 2012; Luo et al., 2016), *Bactrocera tryoni* (Hurst et al., 2024; Tomerini et al., 2024), *Bactrocera jarvisi* (Tomerini et al., 2024; Welty Peachey et al., 2024), and *Zeugodacus cucurbitae* (Miller et al., 2022). Key to tracking the latter three species has been the fabrication of tags with antennas made of superelastic nitinol wire, resulting in a tag that is light (<1 mg), flexible, and does not tangle.

The target insect for tracking in this study is Qfly, a major horticultural pest in eastern Australia, which attacks a wide range of fruit crops (Clarke et al., 2011; Drew, 1989; Yonow & Sutherst, 1998) and restricts interstate and international trade (Dominiak & Daniels, 2012; Sutherst et al., 2000). With the recent restrictions on dimethoate and fenthion use, on-farm control of *B. tryoni* is now more reliant on integrated pest management (IPM) strategies (Clarke et al., 2011; Dominiak, 2019), which may include the use of semiochemicals for both monitoring and control, protein baits containing toxicants, field sanitation, sterile insect technique (SIT), male annihilation technique (MAT), biological control via natural enemies such as parasitoids, and areawide management (applying IPM techniques over a large geographical area) (Kim & Kim, 2016; Vargas et al., 2008). Beyond the farm level, government agencies deploy trapping networks for early detection of invasive tephritid pests (Clarke, 2019) and when fruit flies are detected, delimitation and quarantine efforts are often initiated to avoid fly establishment (Gilbert et al. 2010; International Plant Protection Convention, 2018; Ormsby, 2021). However, the size of quarantine treatment areas is often difficult to set (Caton et al., 2021; Dominiak & Fanson, 2020) due to factors such as the initial introduction location being unknown, the length of time since the incursion, and critically, the dispersal ability of the pest fly.

Optimizing trapping networks and toxicant baits placement, improving the precision of quarantine deployment, predicting pest outbreaks, and potentially improving SIT are all possible outcomes of having a more complete understanding of fly movement (Caton et al., 2021; Lux, 2014, 2018; Manoukis et al., 2014; Manoukis & Hoffman, 2014). Previously, movement data have been used to optimize IPM control strategies for the brown marmorated stink bug, *Halyomorpha halys* (Morrison et al., 2016) and the spotted wing drosophila, *Drosophila suzukii* (Rice et al., 2017). Although there is some information about Qfly population dispersion in nature, little is known about the movements of individual Qflies in their environment (Dominiak, 2012; Dominiak & Fanson, 2020). Determining individual Qfly movement parameters will enhance our understanding of pest distributions, which may lead to improvements in large-scale surveillance and invasion countermeasures as well as farm-level IPM strategies.

A promising method to optimize fly detection and control measures is the application of individual-based ("agent-based") models (ABS). The ABS are simulations of autonomous individuals (agents) that interact with the environment and other agents (Railsback & Grimm, 2012). Previous ABS have addressed management and eradication of tephritids (Lux, 2014, 2018; Manoukis & Hoffman, 2014) including Qfly (Dominiak & Fanson, 2023; Schwarzmueller et al., 2019). Trapping models particularly benefit from realistic movement simulation (Branco et al., 2006; Drummond & Collins, 2020; Manoukis et al., 2014), as target insect movement substantially contributes to the probability of capture (Caton et al., 2021; Miller et al., 2015). Real-world estimates of certain parameters, such as fly step-distances, flight directionality, and movement rates, would especially benefit spatially explicit models of fruit fly movement.

Previous HR field studies of mid-sized tephritids (Hurst et al., 2024; Miller et al., 2022; Welty Peachey et al., 2024) have included prodding flies that remain stationary for 5 min to induce movement. This methodology was employed to increase the number of movement steps during an observation period. Although this method makes data collection easier and faster, it is also less natural and precludes the determination of movement speed.

This study aimed to use HR to determine movement parameters for wild male Qflies in papaya (*Carica papaya*, Caricaceae) fields with a focus on wind effects (Experiments 1 and 2) and natural (not induced) movement (Experiment 2). Experiment 1 involved nearly constant fly observation (flies were not tracked while in flight) with flies disturbed to induce movement in a high-density papaya field (also used for a similar study the previous year). Experiment 2 was conducted in a low-density papaya field with nearly constant fly observation and no artificial fly disturbance. Analysis of the recorded movement data provided Qfly step distances, turning angles, speed, and flight directionality with respect to the wind.

MATERIALS AND METHODS

Insects

Wild male *B. tryoni* were collected on the grounds surrounding the Department of Agriculture and Fisheries facility in Mareeba, QLD, Australia (–17.007706, 145.430037), with modified Lynfield traps containing cuelure [4-(3-oxobutyl)phenyl

acetate]. Traps were hung at a height of approximately 1.8 m at least 5 m apart (vegetation permitting). Flies were collected daily at approximately 9:00 hours. Flies were trapped, tagged, and tracked within the same day. Flies that were collected but not immediately tagged were held in BugDorm-4F3030 insect rearing cages (32.5 × 32.5 × 32.5 cm; BugDorm, Taichung, Taiwan) and supplied with water and sugar cubes in a climate controlled laboratory (26°C ± 1°C, ~70% r.h., natural light ~L11:D13). Flies that failed to exhibit flight behavior in cages after initial capture were not tagged.

HR tag fabrication and attachment

Dipole HR tags were fabricated from a Schottky diode (RECCO, Lidingö, Sweden) and straight annealed 0.0254-mm-diameter superelastic nitinol wire purchased from Fort Wayne Metals (Fort Wayne, IN, USA) as outlined by Miller et al. (2022). Briefly, two 4 cm lengths of wire were attached to the diode with UV-activated adhesive (Bondic, Niagara Falls, NY, USA). Electrical connections between the wires and the diode contacts were secured using conductive silver paint (GC Electronics, Rockford, IL, USA). Individual tags weighed approximately 0.8 mg. The signal strength of each tag was tested after assembly using a HR transceiver unit (R9) purchased from RECCO. Tags that returned the strongest signals were subsequently attached to flies for use in tracking.

To prepare for tag attachment, flies were immobilized by placing them in a refrigerator (~4°C) for 10 min or until cessation of movement. Individual flies were then held by the legs, and a tag, dipped in the UV-activated adhesive, was positioned in a longitudinal orientation on the dorsal surface of the thorax before being cured with light from a UV LED. Care was taken not to glue the wings or the head during tag attachment. Tag diodes were painted distinct colors using nail polish to allow visual identification of specific flies in the field.

General tracking protocol

Field location of flies with HR was achieved by searching an area to which a fly was visually observed to have flown to (when possible) or by searching in a regular pattern from the last known location. If a potential landing site was detected visually, the surrounding trees and ground were searched until a signal was detected. During searching, the RECCO unit was rotated and moved from side to side to maximize signal detection by aligning the transceiver with the tag attached to the fly. Under optimal conditions, without vegetation interference, alignment of the RECCO unit with the tag yielded a maximum detection range of approximately 20 m with a strong signal generally detected at approximately 10 m. However, in the papaya field under field tracking conditions, detection distances were around 3 m due to suboptimal tag/transceiver alignment and interference from vegetation.

When a signal was found, the time was recorded, and the tree was searched. Once the fly was visually detected, a second time was recorded, and the location was marked using flagging tape. If a strong signal was found and the fly took flight before a visual observation was made, the suspected location was still flagged as a step based on the strong signal. The length of the steps was recorded at ground level, and the direction was marked for each step using a compass. Particularly for longer flights and for flies that took longer to locate, it is possible that flies might go through several flight/land cycles before being detected. Thus, "step," most accurately, is the distance between successive recorded positions.

Wind speed and direction were continuously measured using Kestrel 3550FW weather meters (Boothwyn, PA, USA) mounted on tripods approximately 1.3 m above the ground. Two weather meters were used: one located several meters upwind of the release podium (to avoid signal interference) and a second downwind at the edge of the field. The sampling rate was every 5 s (recorded to a Bluetooth-connected phone).

Study site

Experiment 1 was conducted in a subsection of a larger papaya field in Paddy's Green, QLD, Australia (several hundred meters surrounding the release point: −16.989040, 145.319282). The release point was a cardboard box with a roughly 0.14 m^2 surface area (30 × 45 × 25 cm) placed between several papaya trees. Papaya trees in the study area were planted in raised double rows with approximately 3 m between trees (Figure S1A). Each double row of trees was separated by a roughly 2 m wide dirt/mowed-grass access track. Trees ranged in height from 2.5 to 3.5 m, with the foliage of one tree nearly touching that of the neighboring tree within a row. Papaya trees in this study area were both planted in higher density and had greater foliar density than those of Experiment 2. Ground cover plants were short (generally less than 30 cm) and sparse throughout the field. The study field area was bordered on the north by trees and scrub, whereas older, taller papaya lay to the south.

Experiment 2 was conducted in a subsection of a larger papaya field (several hundred meters surrounding the release point: −16.974381, 145.370700) in Paddy's Green, QLD, Australia approximately 6 km east of the field used for Experiment 1. The release point was the same cardboard box as in Experiment 1 placed between several papaya trees. The release point location was flagged at the beginning of the study so that it was placed in the same approximate location for all trials. Papaya trees in the study area were planted in single rows with approximately 3–4 m between trees (Figure S1B). Each row of trees was separated by a roughly 3 m wide dirt/mowed-grass track. Trees ranged in height from roughly 3–4 m with crown foliage roughly 2–3 m in diameter. Tree foliage was generally separated from neighboring trees by at least 1 m. Ground cover plants were short (generally less than 30 cm) and sparse

throughout the field. The study field area was bordered on the west by a dirt access road with cattle grazing areas on the other sides.

Both experiments were conducted between 9:30 and 16:30 hours. Weather conditions during this time were generally sunny with a mean daily high temperature of 27.3°C ± 0.3°C.

Experiment 1—Induced movement (13, 15–16, 20–23, and 30 June 2023)

Experiment 1 investigated the continuous movement of tagged Qflies in the papaya study field over 9–16 steps (flights). Tagged flies were released one at a time. If a fly did not take off within 5 min of being released, a piece of grass was used to encourage flight. If no flight occurred with prodding, the fly was designated a non-flier, collected, and placed in a separate cage.

Flies were tracked one at a time after being released into the field. After release, tagged flies were tracked through the field with landing locations (specific tree or grassy area) recorded after each flight. At most landing locations, the fly was visually located; however, in some instances, the fly took flight before a visual confirmation was possible, and the presence of the fly was identified by signal detection only. Flies were allowed to rest for 5 min following each flight before prodding to induce further movement. If a fly had not flown again after 5 min, the surrounding foliage was disturbed to induce flight. Flies with at least five recorded flights were used in the analysis. Up to 16 steps were recorded for each tagged fly. When possible, flies were recaptured and removed from the field after 10–16 recorded flights. Step-distances (flight distances), flight directionality (angle from take-off to landing), and turning angles (angle between successive flight directions) were calculated from recorded fly positions. Tracking a single fly to ≥10 steps generally required about 1 h. The number of flies tracked per day ranged from 2 to 5, with a total of 22 flies released during the experiment.

Experiment 2—Natural movement (5–6, 10, and 13–14 July 2023)

Experiment 2 was designed to investigate the natural (undisturbed) movement of tagged Qflies over 2–18 steps (flights). The experimental methodology was similar to that used for Experiment 1, with the exception that flies were not induced to move after a 5-min period at a location. At each recorded landing location, flies were either visually monitored by an observer, often sitting in a chair below the tree or from a short ladder, or by periodically sweeping the foliage with a transceiver where the fly was previously observed. Ideally, a fly would be observed taking flight so that a direction could be determined to guide subsequent searching. However, with flies sometimes staying in a location for several hours, it was not always possible to observe the exact moment of take-off. A total of 17 flies were released during the experiment.

Statistical analysis

Flight directions were calculated as the bearing between the take-off point and the landing point, whereas the distance between these two points is presented as the step distance. A turning angle is defined as the angle between two successive steps (Figure 3A). The lower end of the operating range for the Kestrel wind meter is 0.6 m s^{-1} (0.4 m s^{-1} if impeller is already moving). Consequently, wind measurements below this threshold are ambiguous and were subjected to further analysis (details in "Results" section). Ultimately, all wind measurements were used unadjusted. Fly flight direction relative to wind direction (relative angle, β, Figure 5A) was calculated as the difference between the bearing of the fly and adjusted wind direction ($\theta_{wind} - 180°$) such that 0° represents a tailwind and 180° a headwind. All analyses of significance were made at the $\alpha = 0.05$ level. The Watson–Williams test for homogeneity of means was used to determine if the flight directions varied between flies. The Rayleigh test and the Hermans–Rasson test (Landler et al., 2019) were used to determine if flight directions, turning angles, and β were random for a given set of data. Differences in wind direction, flight direction, and β were tested using Watson's two-sample test for homogeneity and the Watson–Williams test for homogeneity of means. All circular statistical analyses were performed using R v.2024.09.0+375 (R Core Team, 2021) packages CircStats (v.0.2-6) (Agostinelli & Agostinelli, 2018), circular (v.0.5-0) (Lund et al., 2017), and CircMLE (v.0.3.0) (Fitak & Johnsen, 2020). Equations for step frequencies versus step distances and all *t*-tests were calculated using Microsoft Excel (v.2108; Microsoft, Redmond, WA, USA). The mean movement rate was calculated by averaging the distance moved (m) between the release and final observation points for each fly, divided by the time (h) between the two observations. Hidden Markov models (HMM) were fit using the R package moveHMM (v.1.9) (Michelot et al., 2016). Initial parameters for the two-state HMM were varied within a biologically relevant range to avoid the optimizer estimates converging to a local maximum (Michelot & Langrock, 2023). Threshold regression analyses were performed using the R package chngpt (v.2023.11-29) (Fong et al., 2017). Discontinuous two-phase models were fitted using the stegmented command.

RESULTS

Twenty male Qflies (out of 22 released) were successfully tracked for 9–16 steps in experiment 1. The majority (94%) of fly landing locations in Experiment 1 were in trees, with rare landings in short or long grass. One instance where a fly landed on a person, and one instance where a fly became entangled in a spider web (subsequently freed by

a researcher) were recorded. Analysis of all flights showed a directional flight bias toward the SW (Rayleigh test: test statistic = 35.37, $p < 0.001$; Hermans-Rasson test: test statistic = 53.00, $p < 0.001$) (Figure 1). Wind directions were variable but generally blew from the N, NE, and E (Figure 1, wind rose at left) with wind speeds predominantly below 1 m s^{-1} (68% of the measurements). Flight angle means for each individual fly were not homogeneous (Watson–Williams test: $F_{19,206} = 7.009$, $p < 0.001$) showing that mean flight directions varied between flies. Additionally, 11 of the 20 flies showed nonrandom flight directionality by Rayleigh test, and 10 of 20 by Hermans–Rasson test.

Fifteen male Qflies (out of 17 released) were successfully tracked for 2–18 steps in Experiment 2. The majority of fly landing locations in Experiment 2 were in trees (89%), with rare landings in short or long grass. Several instances of flies landing on cattle droppings, and one instance of fly remains located after apparent ant predation (only the thorax with

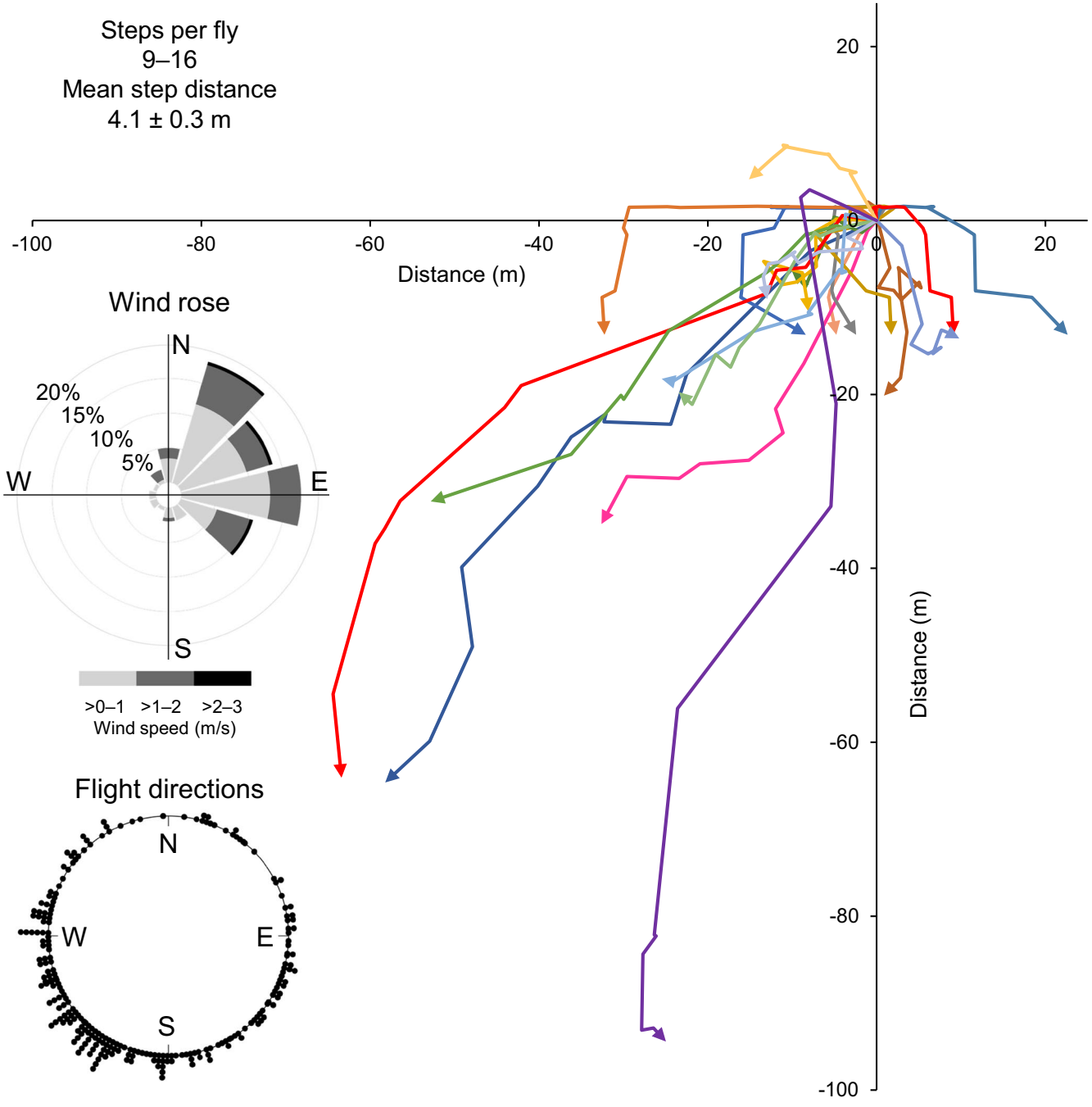

FIGURE 1 Harmonic radar tagged *Bactrocera tryoni* male flight tracks for experiment 1 (induced movement) in a papaya field. Colored arrows represent a series of 9–16 flights for a single tagged fly. When all flights were taken together (inset bottom left), flight directions were not homogeneous but instead showed strong directionality (Rayleigh and Hermans–Rasson tests: Both $p < 0.05$). Each dot represents a single move by an individual insect. The wind rose (inset center left) shows wind directions and speeds at the time of each Qfly flight. Step distance: Mean ± SE.

tag still attached was discovered) were recorded. Analysis of all flights showed a directional flight bias toward the W (Rayleigh test: test statistic = 22.96, $p < 0.001$; Hermans–Rasson test: test statistic = 23.18, $p < 0.001$) (Figure 2). Wind directions were generally from the E (Figure 2, wind rose at left) with wind speeds of predominantly 1–3 m s^{-1}. Flight angle means for each fly were not homogeneous (Watson–Williams test: $F_{14,80} = 3.667$, $p < 0.001$), showing that mean flight directions varied between flies. Additionally, 5 of the 15 flies showed non-random flight directionality by Rayleigh test and 6 by Hermans–Rasson test. The lower proportion of non-random flights is likely due to the lower number of recorded flights (lower test power).

Combined turning angles for Experiment 1 (prodded movement; Figure 3A,B) were non-random (Rayleigh test: test statistic = 23.79, $p < 0.001$; Hermans–Rasson test: test statistic = 33.22, $p < 0.001$) as were combined turning angles for Experiment 2 (natural movement; Figure 3A,D) (Rayleigh test: test statistic = 9.87, $p < 0.001$; Hermans–Rasson test: test statistic = 21.11, $p < 0.001$). Both experiments show a pronounced bias toward forward fly movement as the 95% confidence intervals (CIs) for both sets of turning angles include 0°.

Step distances were shorter in Experiment 1 with a mean of 4.1 ± 0.3 m (mean ± SE) and a median of 2.4 m ($n = 225$; Figure 3C), whereas the mean for Experiment 2 was 6.8 ± 0.7 m with a median of 5.6 m ($n = 101$, Figure 3E). The length of movement paths (the sum of all steps taken by an individual fly) was more consistent in experiment 1 (9–16 steps), with paths ranging in length from 14.4 to 120.1 m with a mean of 50 ± 7 m. Movement path lengths for Experiment 2 (2–18 steps) were from 6.2 to 98.0 m with a mean of 47 ± 7 m. Flight distances in both experiments are well-described by the power equations: Experiment 1 step frequency = 0.5327 × step distance$^{-1.461}$ ($R^2 = 0.833$)

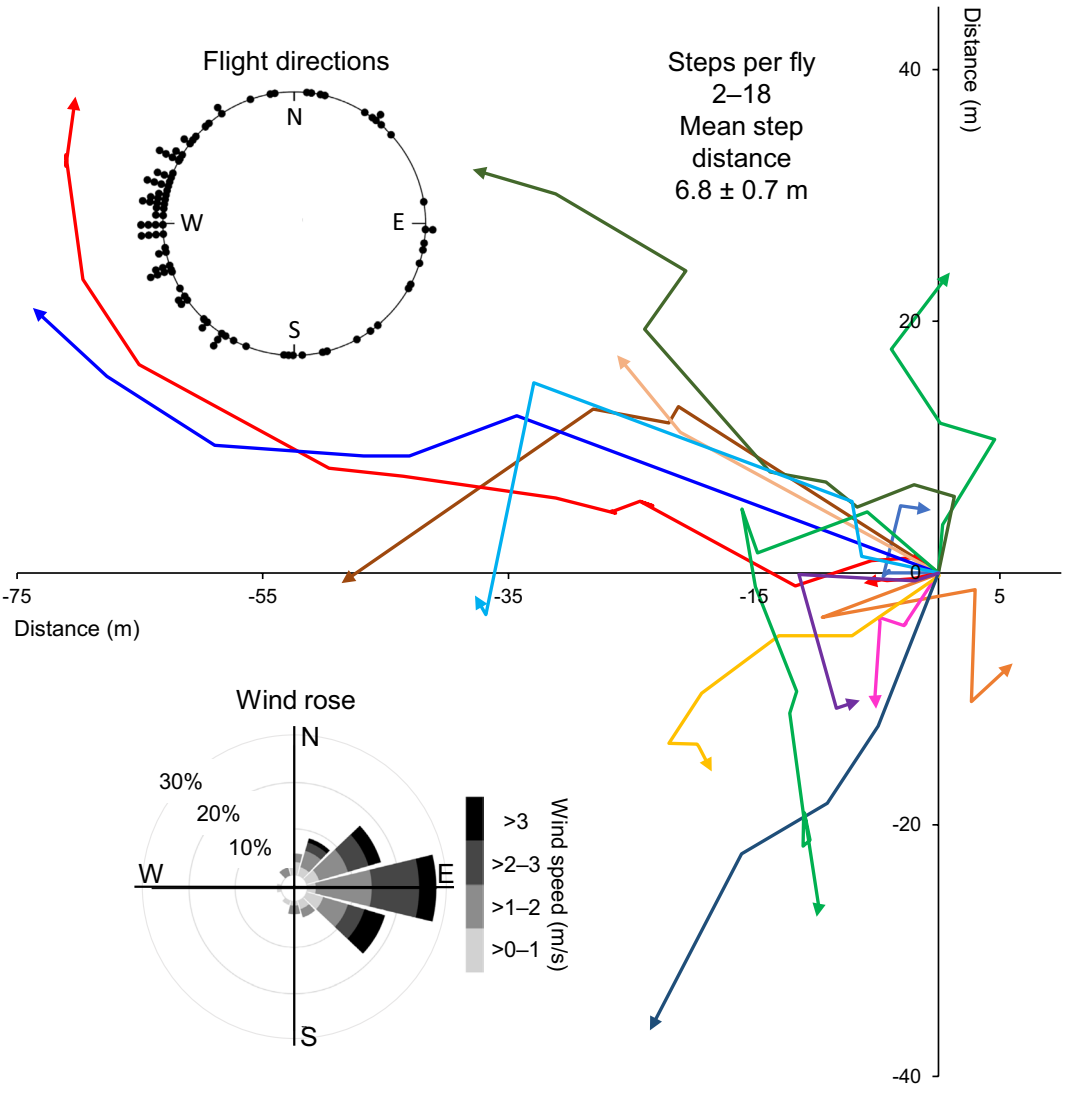

FIGURE 2 Harmonic radar tagged *Bactrocera tryoni* male flight tracks for experiment 2 (natural movement) in a papaya field. Colored arrows represent a series of 2–18 flights for a single tagged fly. When all flights were taken together (inset top left), flight directions were not homogeneous but instead showed strong directionality (Rayleigh and Hermans–Rasson tests: Both $p < 0.05$). Each dot represents a single move by an individual insect. The wind rose (inset bottom left) shows wind directions and speeds at the time of each Qfly flight. Step distance: Mean ± SE.

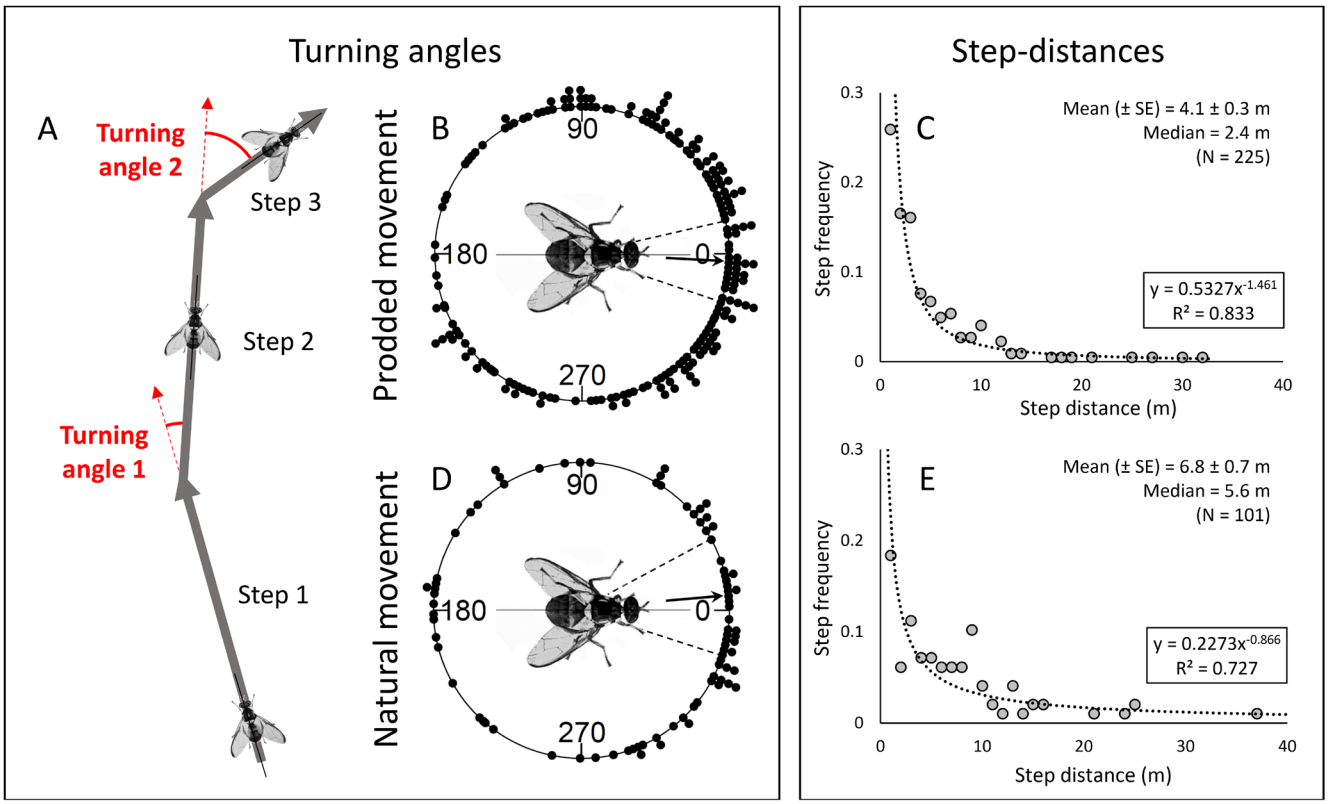

FIGURE 3 Harmonic radar tagged *Bactrocera tryoni* combined turning angles and step distances in a papaya field. (A) Turning angles were calculated as illustrated such that 0° shows no change in direction between two successive steps. Combined turning angles for both (B) prodded and (D) natural movement were non-random and show a pronounced bias toward forward movement (Rayleigh and Hermans–Rasson tests: Both $p < 0.05$). Black arrows show the overall turning angle mean and dotted lines show the 95% CIs for the mean. Each black dot represents a single move by an individual insect. Step-distances for (C) prodded and (E) natural movement were categorized into 1 m intervals for this analysis with the dotted line showing a power function fit to the data.

(Figure 3C); Experiment 2 step frequency = 0.2273 × step distance$^{-0.886}$ ($R^2 = 0.727$) (Figure 3E). Step distances were categorized into 1-m intervals for this analysis.

Observations suggested that shorter step lengths were correlated with more random turning angles, which prompted an analysis with a two-state HMM (Figure 4). The two-state HMM fit to experiment 1 movements showed state 1 with a step distance of 2 ± 2 m (mean ± SD) and a mean turning angle of −0.40 radians with a concentration of 0.16, whereas state 2 had a mean step distance of 7 ± 6 m with a mean turning angle of 0.03 radians and a concentration of 2.57 (Figure 4A,B). The maximum log-likelihood for the 2-state male HMM is −850.4 and the Akaike information criterion (AIC) is 1722.9. The two-state HMM fit to Experiment 2 movements showed State 1 with a step distance of 0.5 ± 0.4 m with a mean turning angle of 2.96 radians and a concentration of 2.65, whereas State 2 had a mean step distance of 7 ± 6 m with a mean turning angle of −0.12 radians and a concentration of 0.98 (Figure 4C,D). The maximum log-likelihood for the 2-state HMM is −423.4 and the AIC is 868.7.

For both Experiments 1 and 2, State 1 steps generally represent within-tree movement, whereas State 2 shows steps between papaya trees. Experiment 1 within-tree movement step distances were 0.7 ± 0.1 m (mean ± SE), whereas between-tree step distances were 6.0 ± 0.4 m. Experiment 2 within-tree movement step distances were 0.41 ± 0.07 m, whereas between-tree step distances were 7.2 ± 0.7 m. Between-tree steps represented 73.5% of all recorded steps in Experiment 1 and 83.3% of steps recorded in Experiment 2.

During Experiment 1, 35.4% of the wind observations fell below the 0.6 m s^{-1} threshold for the anemometer, whereas 19.8% of the observations fell below the threshold in Experiment 2. The higher percentage of values below the threshold in Experiment 1 reflects the overall lower wind speeds observed (0–2.6 m s^{-1}; Figure 1, wind rose) compared to Experiment 2 (0–4.6 m s^{-1}, Figure 2, wind rose). Given the large percentage of measurements that would be lost if these values were simply dropped, these data were inspected more closely to determine the extent to which including values below the threshold might skew the wind/fly directional results. Wind speed data shows a pronounced gap between 0 and 0.6 m s^{-1} (Figures 5G,H and 6G,H) with many instances of low wind speeds recorded as "0 m s^{-1}" values. Given the distribution of wind speeds just above the threshold, it is likely that only ~6% of all measurements are actually 0 m s^{-1} in Experiment 1 and ~3% in Experiment 2. This is supported by observed wind headings changing between most observations, even when all intermittent wind speeds were recorded as 0 m s^{-1}. Further, Qfly flight directions

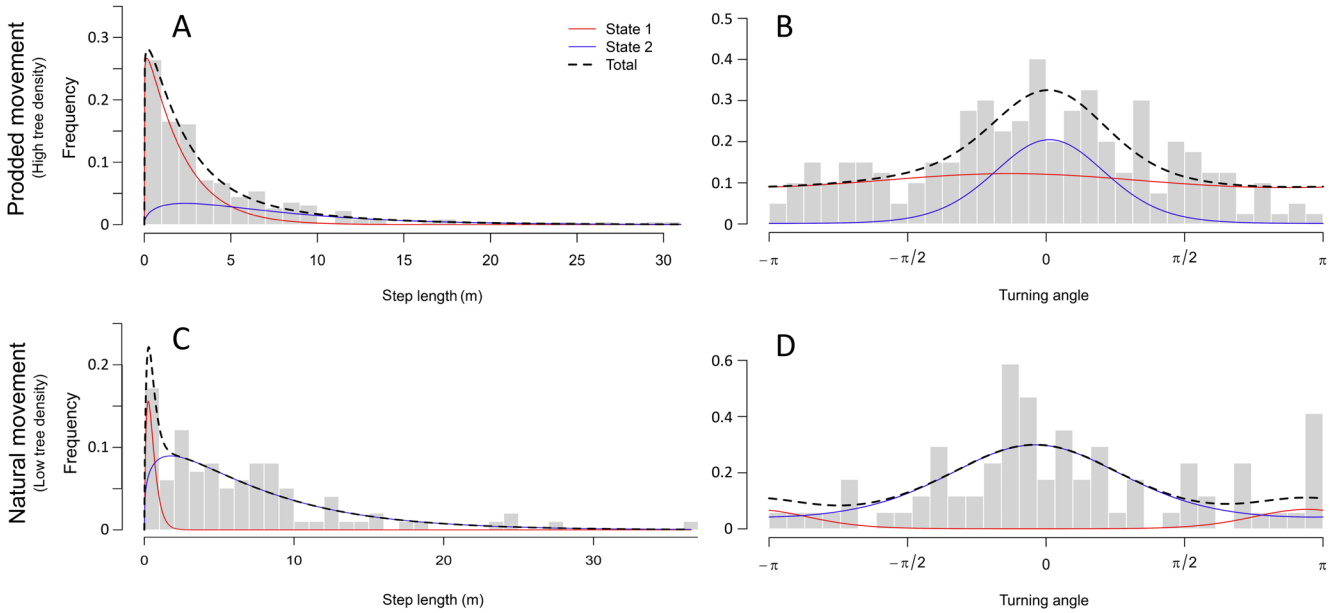

FIGURE 4 Hidden Markov models of (A, B) prodded (experiment 1, higher density papaya trees) and (C, D) natural (experiment 2, lower density papaya trees) *Bactrocera tryoni* movements. The distributions of (A, C) step lengths and (B, D) turning angles are shown for the two-state models. State 1 for both prodded and natural movement correlated with within-tree movements (shorter steps, wider turning angles) whereas state 2 correlates with between-tree movements (longer steps, narrower turning angles).

below 0.6 m s^{-1} from Experiment 1 (Figure S2, upper panels) still show a pronounced flight bias with the prevailing wind. Interestingly, this bias is much less pronounced for flight directions below 0.6 m s^{-1} from Experiment 2 (Figure S2, lower panels), perhaps reflecting the few observations available or a difference in fly behavior (these flies were not prodded to move). We chose to include all the data, not adjusting the wind speeds, with the acknowledgement that an estimated ~3%–6% of wind measurements are inaccurate.

Wind direction affected Qfly movements at both the population and individual level; most flies in both experiments moved with the mean wind direction (Figures 1 and 2) and individual Qfly flights were highly correlated with wind direction at the time of flight (Figures 5 and 6). It is unlikely that flies were simply blown by the wind as not all Qflies moved downwind (Figures 1, 2, 5, and 6). Fly flight direction relative to wind direction (relative angle [β]; Figure 5A) for all experiment 1 movements was not homogeneous (Rayleigh test: test statistic = 16.60, $p < 0.001$; Hermans–Rasson test: test statistic = 24.14, $p < 0.001$), showing movement with the wind (Figure 5B). Additionally, βs for Experiment 1 between-tree movements (Figure 5C) were not homogeneous (Rayleigh test: test statistic = 27.29, $p < 0.001$; Hermans–Rasson test: test statistic = 40.66, $p < 0.001$), showing movement with the wind, whereas βs for within-tree movements (Figure 5D) were homogeneous (Rayleigh test: test statistic = 1.42, $p = 0.24$; Hermans–Rasson test: test statistic = 3.86, $p = 0.32$).

Analysis of Experiment 1 step-distance versus β using a discontinuous two-phase linear model showed a change point at 2.65 m (maximum of likelihood ratio statistic = 19.116, $p < 0.001$). The βs for Experiment 1 movements with step-distances >2.65 m (Figure 5E) were not homogeneous (Rayleigh test: test statistic = 31.68, $p < 0.001$; Hermans–Rasson test: test statistic = 49.97, $p < 0.001$), showing movement with the wind whereas βs for step-distance movements ≤2.65 m (Figure 5F) were homogeneous (Rayleigh test: test statistic = 1.63, $p = 0.196$; Hermans–Rasson test: test statistic = 10.32, $p = 0.069$). Interestingly, the 95% CIs for β in Figure 5B,C,E do not include 0°, indicating a slight movement bias to the left of the wind direction in this context. Wind speeds recorded for Experiment 1 showed a weak negative linear relationship with β (Figure 5G; $R^2 = 0.039$) and a weak positive relationship with step-distance (Figure 5H; $R^2 = 0.047$).

The βs for all Experiment 2 movements were not homogeneous (Rayleigh test: test statistic = 25.41, $p < 0.001$; Hermans–Rasson test: test statistic = 40.68, $p < 0.001$), showing movement with the wind (Figure 6B). The βs for Experiment 2 between-tree movements (Figure 6C) were not homogeneous (Rayleigh test: test statistic = 31.00, $p < 0.001$; Hermans–Rasson test: test statistic = 46.53, $p < 0.001$), showing movement with the wind; whereas βs for within-tree movements (Figure 6D) were homogeneous (Rayleigh test: test statistic = 0.25, $p = 0.95$; Hermans–Rasson test: test statistic = 6.11, $p = 0.17$). Analysis of Experiment 2 step-distance versus β using a discontinuous two-phase linear model showed a change point at 0.98 m (ratio statistic = 17.9, $p = 0.003$). The βs for Experiment 2 movements with step-distances >0.98 m (Figure 6E) were not homogeneous (Rayleigh test: test statistic = 33.13, $p < 0.001$; Hermans–Rasson test: test statistic = 48.74, $p < 0.001$), showing movement with the wind, whereas βs for step-distance movements ≤0.98 m (Figure 6F) were

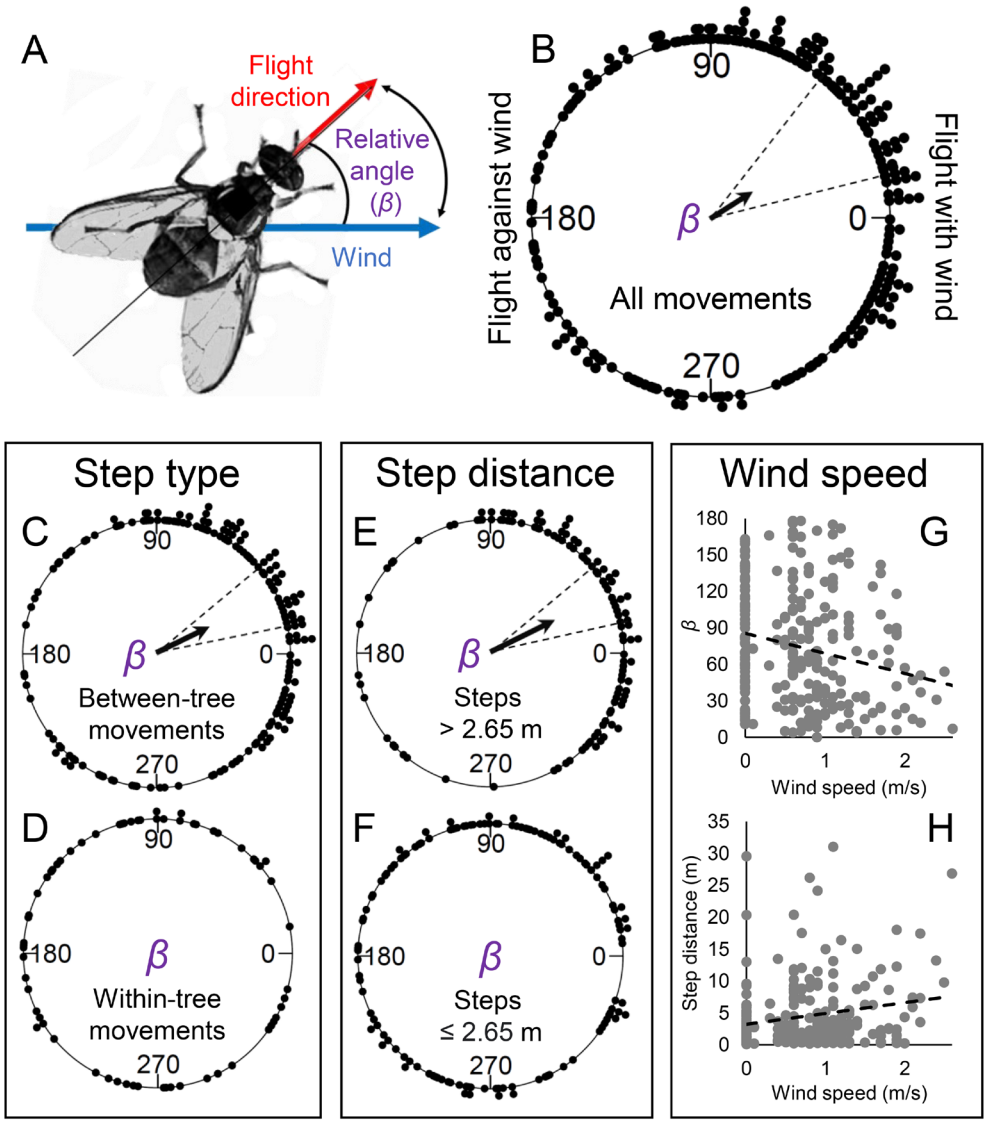

FIGURE 5 Wind directions relative to *Bactrocera tryoni* flight trajectories (β) for experiment 1 (prodded movement). (A) The βs were calculated as illustrated such that 0° indicates a tailwind whereas 180° indicates a headwind. (B–F) Black arrows show the overall mean value of β; arrow lengths ($\bar{r}$, mean resultant length) show the degree of clustering around the mean; each black dot represents a single move by an individual fly; and dotted lines show the 95% CIs for the mean. Movements for (B) all *B. tryoni*, (C) between-trees, and (E) step-distances longer than 2.65 m were each shown to be non-random, showing a strong correlation of fly and wind directions (Rayleigh and Hermans–Rasson tests: Both $p < 0.05$). Movements (D) within-trees and (F) shorter step distances were found to be random, showing a limited correlation between fly trajectories and wind directions (Rayleigh and Hermans–Rasson tests: Both $p > 0.05$). Wind speed had (G) a weak negative linear relationship with β and (H) a weak positive linear relationship with step distance with the dotted line showing a linear function fit to the data.

homogeneous (Rayleigh test: test statistic = 1.58, $p = 0.548$; Hermans–Rasson test: test statistic = 6.35, $p = 0.138$). Only the 95% CIs of β for steps >0.98 m (Figure 6E) do not include 0°, indicating a slight movement bias to the right of the wind direction in contrast to Experiment 1. Wind speeds recorded for Experiment 2 showed a weak negative linear relationship with β (Figure 6G; $R^2 = 0.010$) and a weak positive relationship with step-distance (Figure 6H; $R^2 = 0.028$).

The mean rate of movement per fly for Experiment 2 (natural movement) was $19 \pm 3\,m\,h^{-1}$ (mean ± SE; $n = 15$). Individual fly movement speeds ranged from 1.2 to $48.5\,m\,h^{-1}$. The mean time between Qflies movements was 23 ± 4 min, with the longest period a Qfly remained in the same location reaching 3 h 11 min. The mean tracking time per fly was 2 h 32 min ± 25 min. Per fly tracking times ranged from 10 min to 5 h 39 min.

DISCUSSION

Prodding versus natural movement methods

Despite differences in tracking protocols (induced vs. natural movement) and vegetation structure (high vs. low papaya planting density), movement parameters observed in Experiments 1 and 2 were similar. Step

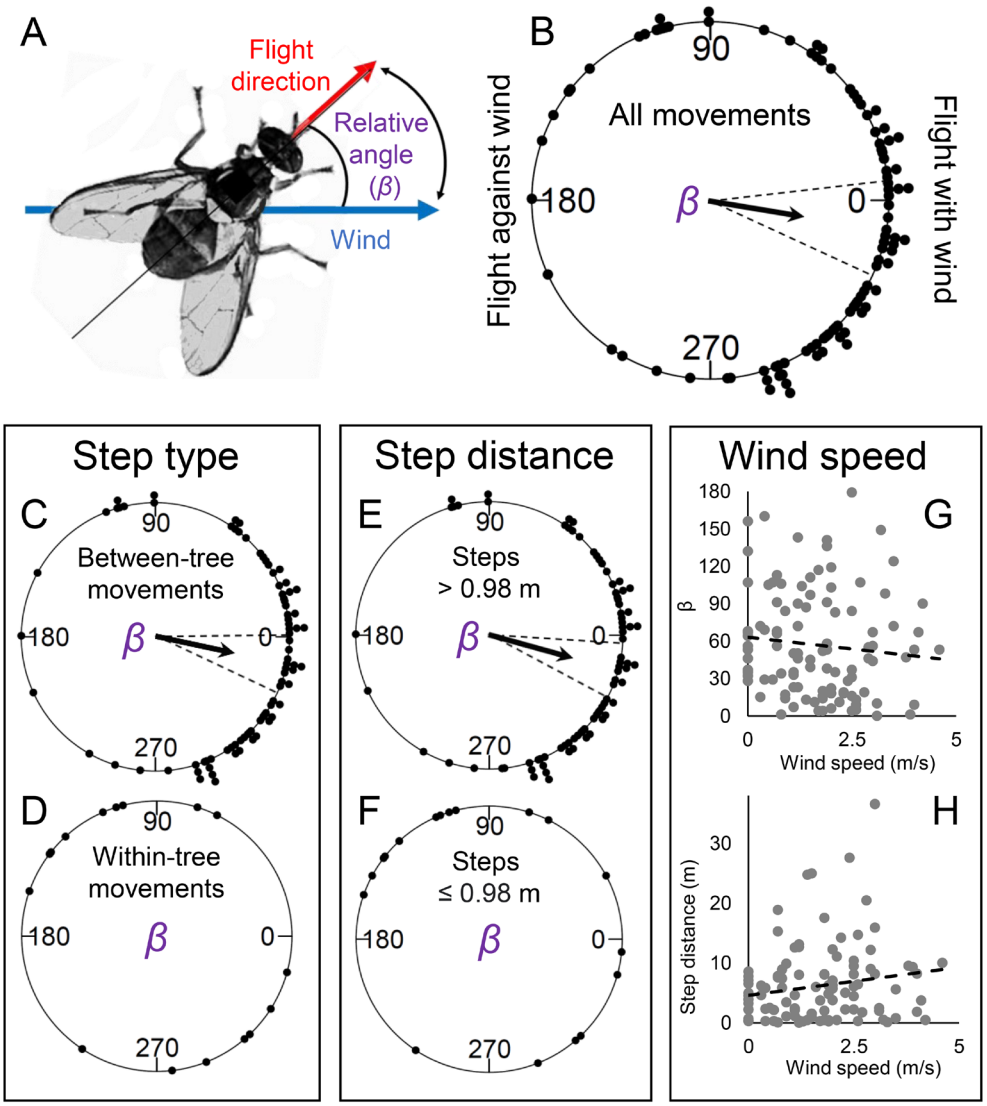

FIGURE 6 Wind directions relative to *Bactrocera tryoni* flight trajectories (β) for experiment 2 (natural movement). (A) The βs were calculated as illustrated such that 0° indicates a tailwind whereas 180° indicates a headwind. (B–F) Black arrows show the overall mean value of β; arrow lengths ($\bar{r}$, mean resultant length) show the degree of clustering around the mean; each black dot represents a single move by an individual fly; and dotted lines show the 95% CIs for the mean. Movements for (B) all *B. tryoni*, (C) between-trees, and (E) step-distances longer than 2.65 m were each shown to be non-random, showing a strong correlation of fly and wind directions (Rayleigh and Hermans–Rasson tests: Both $p < 0.05$). Movements (D) within-trees and (F) shorter step distances were found to be random, showing a limited correlation between fly trajectories and wind directions (Rayleigh and Hermans–Rasson tests: Both $p > 0.05$). Wind speed had (G) a weak negative linear relationship with β and (H) a weak positive linear relationship with step distance with the dotted line showing a linear function fit to the data.

distances for Experiment 1 were slightly shorter than those in Experiment 2, likely due to a combination of higher wind speeds, higher foliar density, which gave flies closer vegetation to land on, longer average resting times, and potential behavioral differences when flights were not initiated by human disturbance. In contrast, turning angles and step distance frequencies, movement within and between trees, and the influence of wind on flight direction were not substantially different between the experiments. This is advantageous for future studies as Experiment 1 was easier and faster to conduct. In other words, Experiment 2 (observations of natural movement) validates that the movement data collected in Experiment 1 are biologically relevant. However, only the natural movement methodology allowed the determination of movement speed.

Movement speed

Measurements of step distances, turning angles, and speed are needed for an in-depth description of the movement patterns of an individual. The first two parameters, step-distance and turning angle, have been previously reported for tephritid fruit flies from studies using HR (He et al., 2019; Hurst et al., 2024; Miller et al., 2022; Welty Peachey et al., 2024); however, the speed of insect movement has remained largely unaddressed. He et al. (2019),

studying *B. minax*, did not report on fly movement speed, whereas studies of *B. jarvisi* (Welty Peachey et al., 2024) and *Z. cucurbitae* (Miller et al., 2022) could not give behaviorally relevant speed measurements due to the experimental protocols used (tagged flies in these studies were prodded to induce movement as was done in Experiment 1 in this present work). Whereas Hurst et al., 2024 reported a mean movement speed of (mean ± SE) 1.7 ± 0.5 m h^{-1} for *B. tryoni*, this measurement was derived from periodic observations and therefore reflected a displacement distance, not a measurement of the cumulative distance moved by Qflies, as was recorded in the present study. Interestingly, the movement speed observed in the present study shows Qflies moving at a rate roughly an order of magnitude faster than that reported by Hurst et al. (2024). This difference is likely influenced by several factors, including differences in experimental design (twice daily vs. near constant observation), time of data collection (Hurst et al., 2024 collected data spanning scotophase when Qflies are likely inactive), and to a lesser extent, differences in weather (wind, temperature, barometric pressure, etc.), other environmental conditions, and movement cues (visual, auditory, etc.). Although collection of the movement data allowing the calculation of movement speed was more labor intensive than that collected by Hurst et al. (2024), the quality of the derived speed measure was likely higher, as this approach allowed the collection of continuous data over a period of time when flies are expected to be actively moving. The measurements by Hurst et al. (2024) may reflect the mean movement speed over a 24-h period, whereas the measurements reported from the present study reflect the speed of flies during periods of active movement.

Movement distances

Past research (He et al., 2019; Hurst et al., 2024; Miller et al., 2022; Welty Peachey et al., 2024) and the present study support the prevailing notion that individual tephritid step-distances are fairly short (Dominiak, 2012; Dominiak & Fanson, 2020) (tens of meters not kilometers). Step-distances (m per flight) reported in previous tephritid tracking roughly range from 2 to 6 m per step, with the experiment 1 mean falling in the middle of this range, whereas the experiment 2 mean falls in the upper part of this range.

The relationships between step frequency versus step distance (categorized into 1-m intervals) observed in both experiments are well described by power functions, again similar to what was found previously with *B. tryoni* (Hurst et al., 2024), *Z. cucurbitae* (Miller et al., 2022), and *B. jarvisi* (Welty Peachey et al., 2024), showing that flies generally make short flights within and between nearby trees with less frequent longer flights. Movement data for which a power function is a better fit than an exponential function (as is true here) are typically classified as Lévy walks (Plank et al., 2013). Lévy walks, short random steps with occasional larger steps, are found in many animal movements (Reynolds, 2008, 2013; Wosniack et al., 2017) and have been invoked previously to explain *B. tryoni* movements (Meats & Edgerton, 2008).

Movement directionality

Tracked Qfly showed both biased individual-level flight directions and collective directional biases in turning angles. Additionally, combined absolute flight directions showed directional bias, suggesting that Qflies orient toward environmental directional cues (e.g., visual, light, and wind cues). These individual and collective biases in directional movements are generally similar to those observed with tracked tephritids (He et al., 2019; Hurst et al., 2024; Miller et al., 2022; Welty Peachey et al., 2024). Wind was a factor in the directional movement of at least some *Z. cucurbitae* and *B. jarvisi* (Welty Peachey et al., 2024), whereas *B. minax* movement bias was attributed to flies moving from an orchard into an adjoining forest (He et al., 2019).

Movement and behavioral states/ spatial scales

There appear to be differences between intra-tree (within tree) and inter-tree (between tree) movement behaviors, which were explored using HMM. Whereas HMMs are widely used for analysis of animal movements (Glennie et al., 2023), applying these models to insect movement is more limited (Hannigan et al., 2023; Hurst et al., 2024; Sim et al., 2015; Welty Peachey et al., 2024). Both two-state HMMs derived in this study fit the observed Qfly movement data well, which suggests that Qflies move in qualitatively different manners when taking shorter versus longer steps. State 1 for each experiment showed both shorter step distances and more random turning angles when compared to State 2. State 1 steps likely represent within-tree movements, whereas State 2 steps reflect between-tree movements. The random directionality of shorter steps was also observed previously in Qflies (Hurst et al., 2024) and *B. jarvisi* (Welty Peachey et al., 2024).

Tree density appears to influence both the distribution of step distances between the two states and the ratios (or numbers) of steps within a state. High foliar density increases the proportion of State 1 steps and the range of step lengths for which State 1 is predominant (state 1 > state 2 for step lengths <~5 m, no state 1 steps >10 m). Conversely, low foliar density appears to decrease the proportion of State 1 steps and the range of step lengths for which State 1 is predominant (state 1 > state 2 for step lengths < ~1 m, no State 1 steps >2 m). This suggests that greater foliage density influences Qfly to increase searching behavior (state 1, shorter less directed steps) and not by simply blocking movement. If the latter explanation holds, there should be a higher number of short directionally biased

(state 2) steps in Experiment 1. Inter-tree distance has been shown to influence fly intra- and inter-tree movements for other tephritids, namely the apple maggot (*Rhagoletis pomonella*) (Roitberg & Prokopy, 1982) and the western cherry fruit fly (*Rhagoletis indifferens*) (Senger et al., 2009). In both of these species, increased distance between trees decreased inter-tree movements.

Wind effects

Similar to the HMM indicating that movement parameters derived from the entire data set do not adequately describe the movement of individual Qflies for all behavioral states or at all spatial scales, so too the effect of wind changes with scale or movement type. Both prodded and natural movement directions were strongly correlated with wind direction (β) when moving between trees and taking longer steps but not when moving within trees or taking shorter steps. These results mirror those of Welty Peachey et al. (2024). As suggested by the HMM, the effect of foliar density can again be observed in where the break in β was found with respect to step distance. For Experiment 1 (higher density papaya), the break in β was observed at over twice the distance observed in Experiment 2 (lower density papaya). Again, having larger areas of contiguous foliage appears to lengthen the step distances associated with the HMM State 1 (shorter, undirected movements).

Whereas wind direction has a strong impact on Qfly directional movement, additional cues appear to also be influencing flight directions. This is supported by the observation that 95% confidence intervals (CIs) of multiple βs do not include 0°, indicating a slight movement bias away from the wind direction. This effect was more pronounced in Experiment 1 and might represent movement toward taller trees (tree age and height increased when moving toward the south). Other visual cues could be the angle of the sun, hills, etc. No obvious visual cues were noted in Experiment 1 that would explain the small rightward-of-the-wind bias.

Previous studies have also identified wind speed as an important factor influencing the movement of insects (Bell et al., 2013; Knight et al., 2019; Pasek, 1988). It is therefore interesting that increases in wind speed only slightly increased the correlation between flight and wind directions (β).

Study limitations

An important consideration on the observed Qfly movements in this study is that tracking took place in northern Queensland during the southern hemisphere winter months (dry season, Experiments 1 and 2 were conducted in June and July). Recently, Tasnin et al. (2021) and Clarke et al. (2022) showed that Qflies have a pronounced seasonal reproductive arrest (not breeding during the dry season) and seasonal demographic changes (longer-lived during late autumn and late winter). Insects in reproductive diapause, due to seasonal phenology, may also experience other physiological changes, and perhaps altered movement. As mate searching is a primary driver for male movement, it may be expected that male Qfly movement would decrease when females are unreceptive to mating.

The research outlined in this paper has concentrated on tracking wild male fruit flies, which are easier to catch in male lure-baited traps. Catching wild females is much more difficult, especially during the dry season in north Queensland when populations are low. Welty Peachey et al. (2024) showed only subtle differences in movement parameters between male and female *B. jarvisi* and it is likely that Qfly females will move similarly to male Qflies.

Potential impact

The movement data obtained in this study, including descriptions of movement parameters and the environmental factors that influence dispersal, enable use of more realistic and accurate agent- or individual-based models that can promote the effectiveness of surveillance and control strategies. Models may enhance current surveillance by optimizing delimitation arrays for improved response following a fruit fly incursion and setting quarantine and eradication boundaries more effectively. Control and eradication methods could also be improved by optimizing trap placements and pesticide applications, determining release sites for parasitoids, modeling gene drives in agricultural settings, determining optimal refuge sizes for Bt or RNAi modified crops, and simulating how pest fly behavior may be altered with changing climatic conditions.

Conclusions

This study demonstrates the feasibility of tracking naturally moving individual Qflies (Experiment 2) using small, lightweight HR tags with flexible antennas. Experiment 2 validates that movement data collected in Experiment 1 (prodded movement, easier and faster to collect) are biologically relevant. Movement parameters determined in this study, particularly those relating to wind direction, provide further quantification of Qfly behavior, which may help mitigate the negative impacts of this important horticultural pest.

AUTHOR CONTRIBUTIONS

Ethan R. Moses: Investigation; formal analysis; writing – review and editing. **Meredith G. M. Lehman:** Investigation; formal analysis; writing – review and editing. **Adesola J. Johnson:** Investigation; formal analysis; writing – review and editing. **Allysen M. Welty Peachey:** Investigation; writing – review and editing; formal analysis. **James M. Yoder:** Investigation; writing – review and editing; formal

analysis; methodology; supervision. **Stefano G. De Faveri:** Conceptualization; funding acquisition; writing – review and editing; resources. **Jodie Cheesman:** Supervision; resources. **Nicholas C. Manoukis:** Writing – review and editing; conceptualization. **Matthew S. Siderhurst:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; visualization; writing – review and editing; formal analysis; project administration; data curation; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the USDA, National Agricultural Library, Ag Data Commons (https://doi.org/10.15482/USDA.ADC/26877439.v1). There are no restrictions on data availability.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Experimental site showing typical foliar density and access track width. (A) The high-density papaya field was planted with trees in double rows with approximately 3 m between trees (foliage generally touched neighboring trees). (B) The low-density papaya field had trees planted in single well-spaced rows with approximately 3–4 m between trees.

Figure S2. *Bactrocera tryoni* (Queensland fruit fly or Qfly) flight trajectories for Experiment 1 (upper panels; prodded movement) and Experiment 2 (lower panels; natural movement) at differing wind speeds. Each dot represents a single move by an individual Qfly. The lower wind speed threshold limit for the anemometer used in this study is 0.6 m s^{-1}.

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