Impact of intercept trap type on plume structure: a potential mechanism for differential performance of intercept trap designs for *Monochamus* species

Marc C. Bouwer[1,2], Chris J. K. MacQuarrie[2], Oniel J. Aguirre-Gil[3], Bernard Slippers[4] and Jeremy D. Allison[2,5]

[1]Department of Chemistry, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria, 0002, Gauteng, South Africa

[2]Natural Resources Canada Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen St. E., Sault Ste. Marie, ON, P6A 2E5, Canada

[3]Department of Crop Protection, School of Agricultural and Veterinarian Sciences, São Paulo State University, Jaboticabal, 14884-900, Brazil

[4]Department of Biochemistry, Genetics and Microbiology, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria, 0002, Gauteng, South Africa

[5]Department of Zoology and Entomology, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria, 0002, Gauteng, South Africa

*Correspondence to Marc C. Bouwer. Email: marc.bouwer@fabi.up.ac.za

Abstract

Studies have demonstrated that semiochemical-baited intercept traps differ in their performance for sampling insects, but we have an incomplete understanding of how and why intercept trap design effects vary among insects. This can significantly delay both the development of new and optimization of existing survey and detection tools. The development of a mechanistic understanding of why trap performance varies within and among species would mitigate this delay. The primary objective of this study was to develop methods to characterize and compare the odor plumes associated with intercept traps that differ in their performance for forest Coleoptera. We released CO_2 and measured fluctuations of this tracer gas from 175-point locations arranged in a 2-by-3-by-2-m grid cuboid downwind of a standard multiple-funnel, a modified multiple-funnel, a panel, a canopy malaise trap, and a blank control (i.e., no trap) in a greenhouse. Significant differences in trapping efficacy between these different trap designs were observed for *Monochamus scutellatus* (Say) and *Monochamus notatus* (Drury) in a field trial. Significant differences were also observed in how CO_2 accumulated in time at different positions downwind among these different trap designs. Turbulent dispersion is the dominant force structuring odor plumes and creates intermittency in the odor plume that is important for sustained upwind flight in insects. Methodological and instrumental limitations resulted in the inability to determine instantaneous plume structures and vortex shedding frequencies for different intercept trap designs. Although we observed differences in the odor plumes emanating downwind of the different intercept trap designs, we were unable to reconcile these differences with capture rates of the different trap designs for *M. scutellatus* and *M. notatus*.

Keywords: Dispersion; Forest Coleoptera; Insect traps; *Monochamus*; Pest management; Pheromone plume; Surveillance

Key message

1. A mechanistic understanding of why intercept trap designs differ in their performance among taxa and habitats would facilitate development and optimization of survey and detection tools.

2. Plume structure downwind of four different trap designs was observed to differ.

3. These differences may influence how insects perceive and respond to different intercept trap designs.

4. We were unable to reconcile observed differences in plume structure with differences in capture rates for *M. scutellatus* and *M. notatus*.

Introduction

Surveys of forest insect pests attempt to monitor populations by sampling the insect or quantifying the damage they cause. Surveys that target the adult stage of an insect often use semiochemical-baited flight intercept traps because they are relatively inexpensive to deploy, particularly in remote locations, and are simple to maintain. Moreover, traps can be 'tuned' to capture a single species or multiple species depending on the semiochemicals used to bait the trap. The performance of semiochemical-baited flight intercept traps (i.e., impact of flight intercept trap design on numbers captured) is a function of the probability of capture of the target taxon, the population density of the target taxon and trap placement relative to target taxon distribution. Efforts to develop and improve survey and detection programs have focused on improving the probability of capture and/or number captured of target taxa, for instance, by increasing the active space of flight intercept traps or improving the capture and retention efficiency of traps. For example, the abundance and diversity of Cerambycidae caught by flight intercept traps are affected by quantitative and qualitative changes in the semiochemicals used to bait traps (e.g., Allison et al. 2004; Allison et al. 2012), trap type and design (Chénier and Philogene 1989; de Groot and Nott 2001; McIntosh et al. 2001; Morewood et al. 2002; Allison et al. 2014; Dodds et al. 2015; Allison and Redak 2017) and where traps are placed along environmental gradients (Allison et al. 2018; Ulyshen and Sheehan 2019).

A recent meta-analysis of the literature on trapping bark and woodboring beetles observed patterns in trap design effects (e.g., trap type, wet vs. dry cup, presence/absence of a trap surface lubricant) on the capture of forest Coleoptera. It also observed a significant amount of heterogeneity in the effects of these factors that was only partially explained by variation among guilds and families (Allison and Redak 2017). The existence of large amounts of

unexplained variation in patterns of effects within guilds and families of forest Coleoptera is an impediment to the development of effective survey and detection programs. For example, this unexplained variation reduces the accuracy of a priori predictions of which trap design will perform the best for a given pest. This can delay the development of effective survey and detection programs by years. These delays can result in increased damage and losses and outright failure of management programs in cases where early detection is critical.

The development of survey and detection programs is also impeded by the lack of consistency in trap performance in the existing literature. For example, higher abundance of longhorned beetles (Coleoptera, Cerambycidae) captured in panel traps than in multiple-funnel traps (McIntosh et al. 2001), no difference in captures between panel traps and multiple-funnel traps (de Groot and Nott 2003) and lower captures in panel traps than in multiple-funnel traps (Allison et al. 2014) have all been reported. As a result, the development of new survey and detection tools for forest Coleoptera is still a trial-and-error process for each taxon of interest. This approach is costly both in terms of the time required to develop and optimize survey programs for emerging pests and the level of damage realized before management programs can be implemented. To resolve these issues, a mechanistic understanding of how and why the most effective trap design varies among taxa and habitats is required.

Among the factors known to impact the abundance and diversity of Cerambycidae captured by intercept traps, trap design is the most studied (Allison and Redak 2017). Variation in the performance of intercept trap designs for sampling forest insects has most commonly been attributed to more attractive traps having a more prominent visual silhouette (Chénier and Philogene 1989). The differences in the relative performance of intercept trap designs for Cerambycidae observed in some studies are consistent with this hypothesis (McIntosh et al. 2001). Others observe no difference (de Groot and Nott 2003) or the opposite pattern, i.e., traps with less prominent silhouettes outperforming those with more prominent silhouettes (Allison et al. 2014)—and are not consistent with this hypothesis.

Research on other insect orders shows that orientation of male moths along pheromone plumes (Mafra-Neto and Cardé 1994; Vickers and Baker 1994) and female mosquitoes along CO_2 and host kairomone plumes (Geier et al. 1999; Dekker et al. 2001) is influenced by the fine-scale distribution of odorant (i.e., plume structure). Few studies have empirically examined the impact of trap design on the plume structure of odorants released from intercept traps, but impacts of trap design on plume structure consistent with differences in trap performance have been reported. For example, Lewis and Macaulay (1976) used ‘smoke’ as a tracer gas to characterize plumes emanating from different trap types and attributed differences in numbers of male pea moths captured to differences in trap odor plume boundaries and internal turbulent structures. Further, behavioral studies with the common furniture beetle, *Anobium punctatum* De Geer, the bark beetle predator *Rhizophagus grandis* Gyllenhaal and the gypsy moth, *Lymantria dispar* (Linnaeus) all suggest that plume structure and not visual stimuli (e.g., trap silhouette) influences flight behavior (Wyatt et al. 19931997; Willis et al. 1994).

The objectives of this study were to develop methods to characterize and compare odorant plume structure variation among different intercept trap designs and to determine whether the observed differences were consistent with differences in trap performance for Cerambycidae. Specifically, we compared the performance of four intercept trap designs: a standard multiple-funnel trap (Lindgren 1983), a modified multiple-funnel trap (Miller et al. 2013), a panel trap (Czokaljo et al 2001), and a canopy malaise SLAM trap in a field trial. To explain variation in trap capture, we characterize odorant plume structure variation by measuring the flow of a surrogate semiochemical (CO_2) from each trap design in a greenhouse.

Materials and methods

Trap performance

A field-trapping experiment was conducted to examine the response of flying cerambycids to different intercept trap designs. The four intercept trap designs were: an aerial canopy malaise trap (SLAM, MegaView Science, Taiwan), a standard 8-unit multiple-funnel trap (Synergy Semiochemicals, British Columbia, Canada), an 8-unit multiple-funnel trap modified to shorten the individual funnels to allow wind to pass through the trap between the bottom and top of successive funnels (modified multiple-funnel trap) (Miller et al. 2013), and an intercept panel trap (Synergy Semiochemicals) (Supplemental Fig. S1). Traps were deployed in a linear array of eight replicate blocks of four traps per block (32 traps total). All traps were treated with Fluon (Northern Specialty Chemicals, USA) and were equipped with a wet collection cup containing 150–200 ml of propylene glycol to increase trap performance (Allison et al. 2011, 2016). Traps were deployed in a former harvest block near Aubrey Falls, Ontario, Canada, that had been harvested in the spring of 2012. The harvest block and the adjacent stands were predominately jack pine, *Pinus banksiana* Lambert, with some red, *Pinus resinosa* Solander ex Aiton, and white pine, *Pinus strobus* Linneaus and white spruce, *Picea glauca* Voss. Traps were suspended individually from metal conduit pipe with a 90º bend at the top, with the collection cup of each trap ca. 0.5–1.0 m above the ground. There was a minimum of 30 m between traps and blocks. Species of *Monochamus* were identified using standard resources (Yanega 1996; Lingafelter 2007).

All traps were baited with ultra-high release pouches containing α-pinene (172 ml; chemical purity > 95%, enantiomeric purity 95% (–); release rate ≅ 2 g/day at 20 °C) (Contech Enterprises, British Columbia, Canada) as a representative host plant volatile and bubble cap lures containing the bark beetle pheromones racemic ipsdienol and ipsenol (chemical purity > 98%; release rate ≅ 0.1–0.2 mg/day at 20 °C) (Contech Enterprises) and the cerambycid pheromone monochamol (chemical purity > 95%; release rate ≅ 0.8 mg/day at 20 °C) (Synergy Semiochemicals). Traps were baited on June 23, 2015, and again on July 21, 2015, and collected weekly from June 30 through September 9, 2015, for a total of 11 collections.

Impact of trap design on plume structures

The plume structure of the same four intercept trap designs and a no-trap blank treatment was characterized in a greenhouse (New North Greenhouses, Sault Ste. Marie, Ontario, Canada). The greenhouse (9 by 44 m in length) was equipped with two large fans located at one end. These fans drew air from the outside through two laminizers that were installed over two large louvered windows on the opposite end of the greenhouse (Supplemental Fig. S1). We constructed the laminizers by connecting a series of air-conditioning filters (Duststop Air Filters Inc. product # 64-3416-2, Ontario, Canada) and then securing these to a wooden frame that was sealed with duct tape and plastic sheeting to the front of the windows. The laminizers reduced but did not eliminate turbulence in the greenhouse. We measured air flow rate with a hotwire anemometer (Model HHF-SD1 by OMEGA Engineering, Toronto) at 30 measurement locations spread out evenly in the greenhouse to find a 3-m-long-by-2-m-wide-and-2-m-high cuboid, where the flow rate was least variable from moment to moment. The best location was found to be in the center of the greenhouse approximately 15 m downwind from the louvers, 26 m upwind from the fans and 4.5 m from the side walls. The height above ground of the lowest measurement location was at 0.6 m, and the distance to the roof from the highest measured location was 1.2 m. The flow rate in this area was 0.50 ± 0.36 m/s (mean ± sd, n = 10,647).

We simulated the pheromone plume from an insect semiochemical lure using CO_2 as a detectable gas released from an emitter. The CO_2 gas (Praxair, 99.9%) was supplied from a cylinder connected to copper tubing, and the flow was set through a duel-stage pressure regulator and two additional needle valves downstream in the tubing. The CO_2 was released at a rate of approximately 0.5 l/min (bubble flow meter) for each experiment. To compensate for temperature differences between released CO_2 and the environment, the CO_2 was passed through a copper tubing coil (2 m) placed in a water bath that was held at room temperature before reaching the release point. Although CO_2 is lighter than pheromone molecules, it is the heaviest common atmospheric gas. As a result, we expected that CO_2 would move downwind faster than larger pheromone molecules. The diffusion coefficient, at 25 °C in air, of CO_2 is 0.1573 cm^2/s compared to 0.0417 cm^2/s for *cis*-9-tetradecenyl acetate, a typical moth pheromone (Yaws 2014). Diffusion, however, is not the major factor that forms pheromone plumes. Rather, turbulent dispersion is the major factor, and thus, while CO_2 is not an ideal analog, it is a good and detectable substitute for insect pheromones.

Traps were hung 15 m downwind of the louvers in the greenhouse at a height that placed the CO_2 release point 1.6 m above ground or at the same height as typical lure placement on intercept traps deployed in the field. The CO_2 release point was set in the center of the fourth funnel for the modified 8-unit multiple-funnel trap and on the outside of the fourth funnel for the standard 8-unit multiple-funnel trap. The CO_2 release point was in the center of the cutout bait area for the panel trap and at the top lure hanging position for the SLAM trap. The blank treatment was just the copper tubing without a trap (Supplemental Fig. S1).

We established a three-dimensional sampling grid (the 'cuboid') downwind of the CO_2 release point by first measuring off a 3-m-by-2-m area on the floor of the greenhouse. We then subdivided the area into a 7 × 5 grid by marking sampling locations at 0.5-m intervals

downwind of the release point (x = 0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0) and 0.5-m intervals crosswind of the release point (z = − 1.0, − 0.5, 0,0.5, 1.0). At each grid point on the floor, we further established vertical sampling points 0.5 m and 1.0 m below the plane of the CO_2 release point, and 0, 0.5 m and 0.65 m above the plane of the CO_2 release point (y = − 1.0, − 0.5, 0, 0.5 0.65). This resulted in 175 (7 × 5 × 5) measurement locations in the cuboid. Due to variation in the size of the different traps tested, we placed the CO_2 release point of each trap 10 cm upwind of the cuboid so that it did not interfere with the positioning of the sensor.

We measured the amount of CO_2 at each point in the sampling grid by measuring the concentration of CO_2 using a portable infrared spectrophotometer (Model LI-840A CO_2/H_2O gas analyzer by LI-COR Biosciences, Nebraska). Each time a sample was taken, we held the spectrophotometer's inlet (referred to as the sensor) so it was turned to face the trap and held parallel to the ground. The sensor was held in place by attaching it to a height-adjustable metal stand. We sampled the air at each measurement location at a rate of 1 l/min through Bev-A-Line® tubing into the analyzer cell of the spectrophotometer. Measurements within a plane were made sequentially starting from a corner of the grid, and we sampled all points in the same plane before moving to the next sampling height. Each point was sampled for 60 s at a rate of 1 sample per second (1 Hz). A 15-s time window passed between individual recordings.

Data processing

Field trial Captures per trap of *Monochamus scutellatus* (Say), *Monochamus mutator* LeConte and *Monochamus notatus* (Drury) were summed across collection dates for analysis. One SLAM trap was down at the collection date of August 11, 2015, resulting in an uneven sampling period among traps. To control for this, total captures were converted to weekly captures and weekly trap captures of each species were analyzed separately using a blocked multiresponse permutation procedure (McCune and Grace 2002). All analyses were conducted with PC-ORD 6.0 (MjM Software Design, Gleneden Beach, OR, USA) using Euclidean distances to construct the distance matrix with blocks aligned before analysis (McCune and Grace 2002), and the multiplicity effect was controlled using step-up False Discovery Rate (Benjamini and Hochberg 1995; Garcia et al. 2004).

Plume Structure/Threshold Analysis We determined whether the flow of CO_2 from the emitter to each measurement location was influenced by the shape and contours of the different traps. We used the accumulated CO_2 concentration at each sensor over the recording period. The accumulated CO_2 concentration was defined as the cumulative sum of all CO_2 concentration measurements recorded at each sensor over the complete recording period. This summation allowed for the expression of the CO_2 concentration observed at each location point in the observation grid as increasing with time. This summation was computed for each location, and for each trap type that was tested which included the blank as a control.

We assumed that the trap type would influence the time for a given sensor to accumulate an arbitrary concentration of CO_2. Moreover, the time it takes for each sensor to accumulate an arbitrary CO_2 concentration should also be influenced by the distance of the

sensor from the emitter. Our preliminary examination of the data (Supplemental Figs. S2–S6) also indicated that height above ground of the emitter could influence the time it took for the sensor to accumulate an arbitrary concentration of CO_2, so we included this variable as a factor.

To determine an arbitrary CO_2 concentration to use as a threshold, we opted to use the middle three quantiles of all the observed data. Other thresholds would be valid, but we argue that selecting the middle three values avoids introducing bias that could result from selecting an arbitrary threshold. Once we had determined these thresholds, we used them to extract the three time points at which each sensor had accumulated the specified three concentrations. We found that the threshold concentration was often exceeded between two time points (i.e., between two sensor recordings) so when this occurred we selected the time point immediately after the threshold concentration was achieved. We repeated this extraction step for each sensor recording. Since there were 5 trap types tested (including the blank control), we also repeated the extraction step for each trap type that was tested. This resulted in 175 time points for each quantile threshold, 525 time points (= 175 × 3) for each trap type (one per sensor for each quantile), and 2625 time points (= 525 × 5 trap types) in the final dataset. We used these time points as the response variables in the statistical analyses.

We fit statistical models comparing the effect of the trap type, distance and height above ground of the sensor on the time to accumulate the quantile thresholds. We fit one model for each of the three quantile thresholds resulting in three independent analyses. In these analyses, 'distance' was computed as the linear distance between the emitter and the location of the sensor in the grid. Height above ground was defined as a categorical variable. We first fit simple linear models containing an effect of distance and the interaction of trap type and sensor height which we diagnosed for issues with heterogeneity and non-normality of residuals using graphical methods (Zuur et al. 2009). All models exhibited issues with both heterogeneity and non-normality, which we addressed using generalized least square (GLS) models that incorporated variance functions for the three predictors (Pinheiro and Bates 2000). Once we had developed a satisfactory statistical model, we assessed for the significance of the main effects using ANOVA. We were also interested in the differences among trap types, so when we found a significant effect of trap type on time we performed post-hoc tests using Tukey's Honest Significant Difference test (Tukey 1949) among the different trap types.

All the threshold analyses were performed in the R statistical computing environment version 3.4.3 (R Development Core Team 2017). The threshold analysis was performed using functions in the stats package (R Development Core Team 2017). The GLS models were fit using functions in the NLME package (Pinheiro et al. 2017), and post-hoc tests were done with functions in the emmeans package (Lenth 2018). All threshold analysis code and data were archived on the Dryad digital data repository (Bouwer et al. 2019).

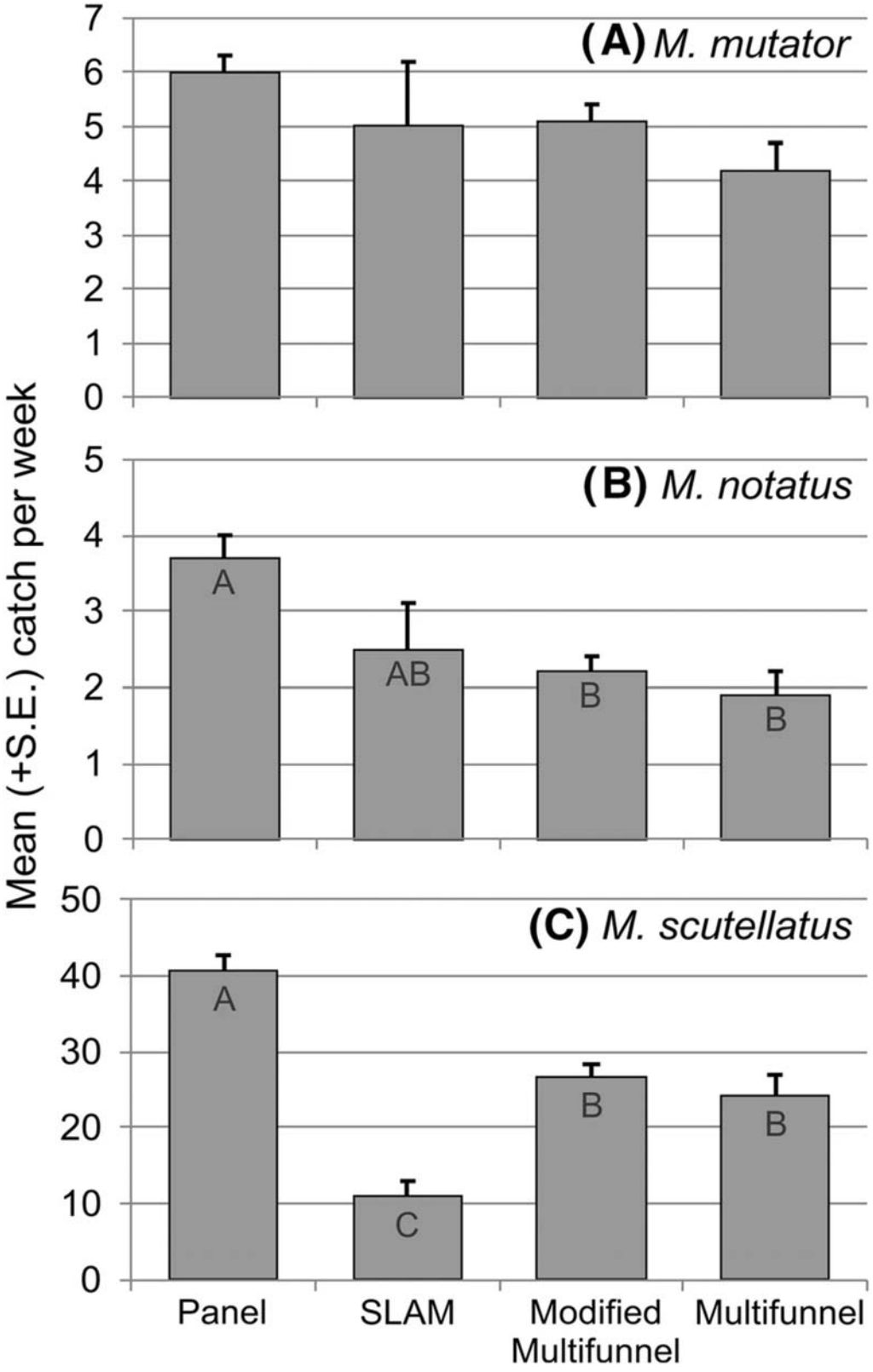

Fig. 1. Trap capture results from the field trial. The graphs display the mean number (± SE) of **a***M. mutator*, **b***M. notatus* and **c***M. scutellatus* captured in each trap design. Note that *y*-axis scale differs between panels. Letters indicate significant difference at $P < 0.05$

Results

Field Trial A total of 11,687 adult *Monochamus* beetles were captured; 9010 *M. scutellatus*, 1772 *M. mutator* and 905 *M. notatus*. There was a significant treatment effect on weekly captures of *M. scutellatus* ($T = -8.98$, $P < 0.001$) and *M. notatus* ($T = -2.79$, $P < 0.05$). There was no treatment effect on the capture of *M. mutator* ($T = -1.85$, $P = 0.053$). Panel traps captured more *M. scutellatus* than all other treatments, and both modified and standard 8-unit multiple-funnel traps captured more *M. scutellatus* than the SLAM traps. Panel traps captured more *M. notatus* beetles than both modified and standard 8-unit multiple-funnel traps (Fig. 1).

Plume Structure/Threshold Analysis The location immediately downwind of the emitter had concentration recordings that were notably higher than those observed at all other locations in the grid. This was attributed to the fact that the sensor was located ca. 10 cm from the emitter and thus received a much more concentrated dose of CO_2 when compared to the other grid locations. Analyses were run with and without (Fig. 2) this datum included; and both analyses resulted in similar statistical results, albeit with some minor changes to the model coefficients (Bouwer et al. 2019).

The summed concentration values ranged from 349 to 28,032 ppm CO_2. The middle three quantiles (25th, 50th and 75th) of these data were at 5470 ppm, 10,739 ppm and 16,002 ppm. We adopted these values as the three thresholds, and then determined the time each threshold was breached at each location in the grid. The time taken to reach the thresholds ranged from 7 to 44 s.

For some trap types, sensors lower in the grid accumulated CO_2 faster, while for others sensors higher up in the grid accumulated CO_2 faster (Fig. 3). This resulted in a significant statistical interaction between height and trap type (Table 1). The SLAM trap accumulated CO_2 faster at the lower sensor positions, especially when compared to the panel and multiple-funnel traps. The multiple-funnel and modified multiple-funnel traps accumulated CO_2 faster at higher positions when compared to the blank recordings.

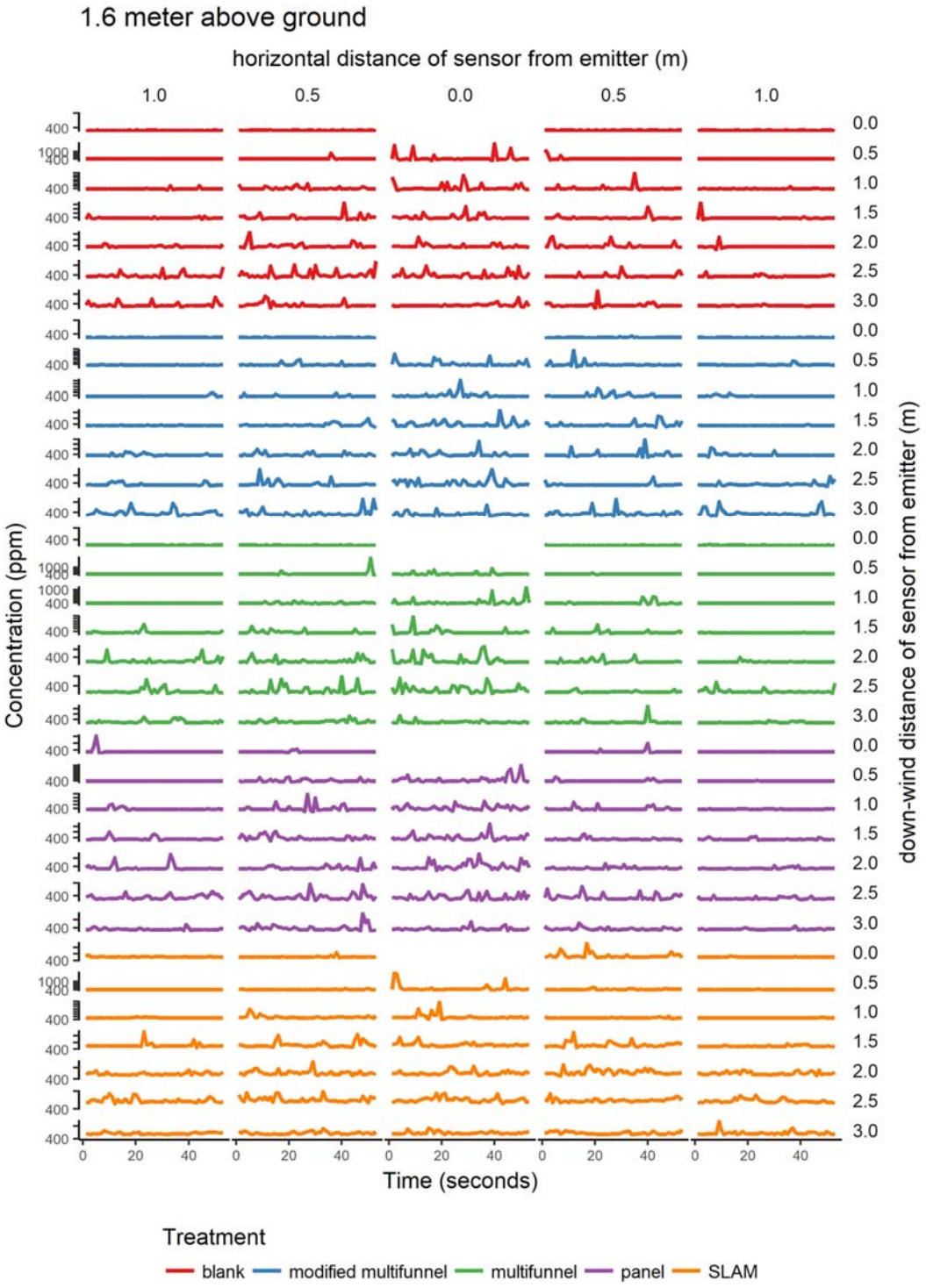

Fig. 2. CO_2 concentrations recorded by a sensor over a 53-s recording period located downwind (rows: downwind of sensor from emitter) and crosswind (columns: horizontal distance of sensor from emitter) of a CO_2 emitter in a blank control (red), a modified multiple-funnel trap (blue), the multiple-funnel trap (green), the panel trap (purple) and a SLAM trap (orange). All readings were taken in the same horizontal plane as the emitter (1.6 m above ground). Note that the scale of the *y*-axis changes over the rows of the plot, in each row the vertical distance between 2 axis tick marks corresponds to 50 units (ppm CO_2). Note how the variability in crosswind CO_2 readings increases for recordings further from the emitter. Background (ambient) CO_2 concentrations ranged between 390 and 450 ppm

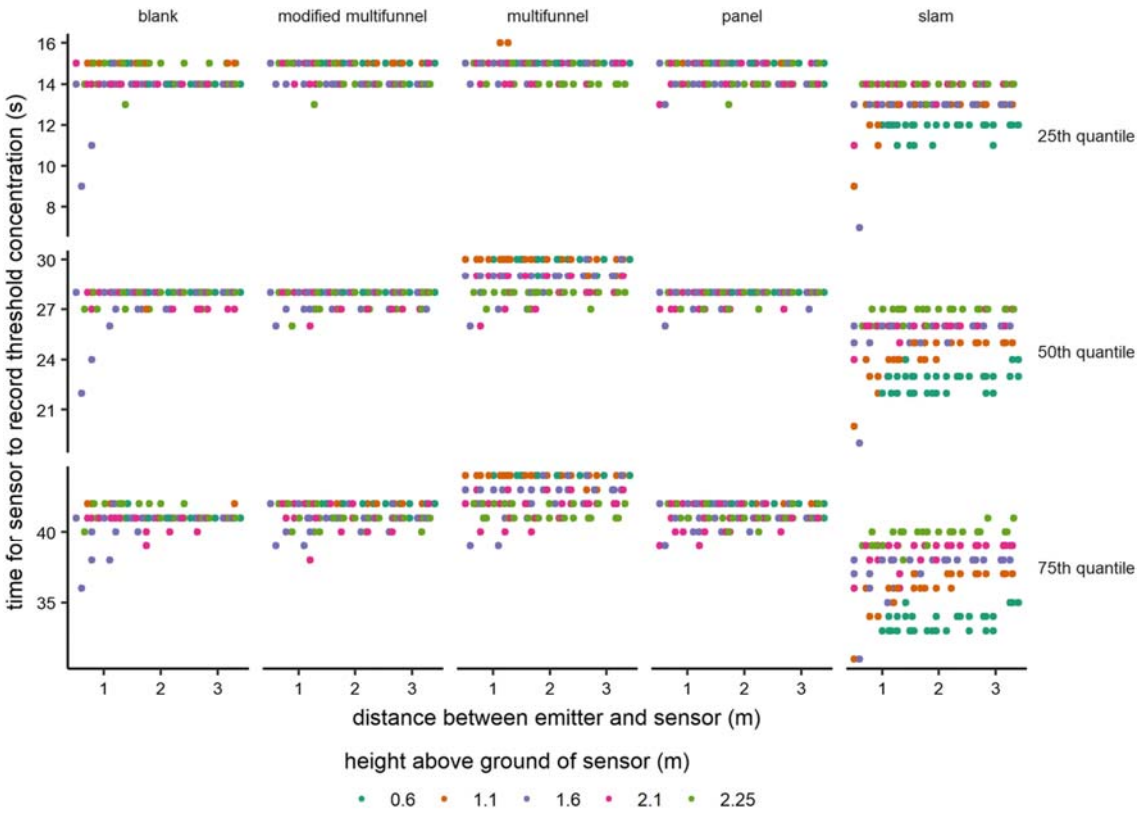

Fig. 3. Time in seconds for sensor to reach threshold concentration of accumulated CO_2 for three different thresholds (rows) from an emitter suspended in air (blank; left column) or placed within one of the four different insect traps. Colors indicate the height above ground of the sensor when the CO_2 readings were taken

Table 1. Summary of ANOVA results for generalized least square models testing the effect of trap type and height above ground on time for a sensor to accumulate a specified concentration of CO_2 released from the emitter

Factor	*df*	*F*	*P*
Threshold 1			
(Intercept)	1	1.5476×10^{6}	<0.0001
Distance	1	1.3873×10^{1}	2.0860×10^{-4}
Trap type	4	1.0685×10^{3}	<0.0001
Height of sensor	4	1.1762×10^{1}	<0.0001
Trap type × Height of sensor	16	6.9169×10^{1}	<0.0001
Threshold 2			
(Intercept)	1	1.4359×10^{7}	<0.0001
Distance	1	6.35485	1.0675×10^{-2}
Trap type	4	2.5155×10^{3}	<0.0001
Height of sensor	4	2.5719×10^{1}	<0.0001
Trap type × Height of sensor	16	7.4765×10^{1}	<0.0001
Threshold 3			
(Intercept)	1	7.8385×10^{6}	<0.0001
Distance	1	1.5299×10^{-3}	9.6880×10^{-1}
Trap type	4	2.8831×10^{3}	<0.0001
Height of sensor	4	5.6787×10^{1}	<0.0001
Trap type × Height of sensor	16	1.6380×10^{2}	<0.0001

Specified concentrations are threshold 1 = 5470, threshold 2 = 10,739 and threshold 3 = 16,002 ppm of the maximum accumulated concentration observed over the entire experiment

Distance from the emitter influenced the time it took at each location to accumulate the threshold concentration (Fig. 3). However, there was not a strong relationship between the two factors such that the effect size was low (Fig. 4). This resulted in a statistically significant effect of distance in some, but not all, models (Table 1). Our statistical model also suggested that there was heterogeneity in the threshold times meaning that traps and sampling heights experienced different variability in the flow of CO_2 from the emitter to the sensor. We noted differences in the time required to reach the threshold values between different trap treatments.

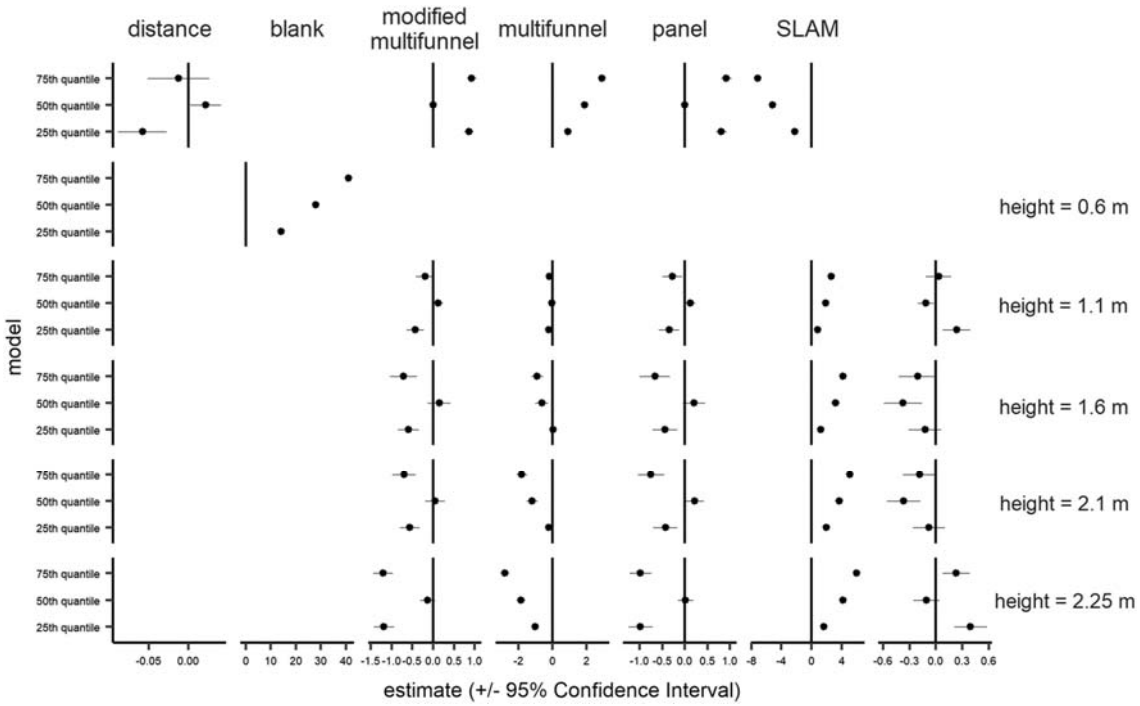

Fig. 4. Model coefficient plot for generalized linear square regressions of the relationship between time for a sensor to record a threshold-accumulated concentration of CO_2 and the distance of that sensor from the CO_2 emitter, the height above ground of the sensor, and the type of insect trap the emitter was placed in (including the blank control). We fit 3 models, one for each threshold value (*y*-axis). The intercept term for each model was determined for height = 0.6 m and the blank control. Coefficients for the main factors in the model are plotted in the upper row and the right-most column. The interaction coefficients are plotted in the central panels. Coefficients where the confidence intervals intersect the horizontal line indicate that term was not significantly different from zero. Details of the model fitting procedure are given in the text

There were differences between all pairwise comparisons of traps, regardless of the threshold (Fig. 5). However, the largest differences were seen in comparisons between the SLAM trap and the other trap types, and the comparison between SLAM trap and the blank control. We also noted that the SLAM trap was most different at the lower positions in the measurement grid (Fig. 5).

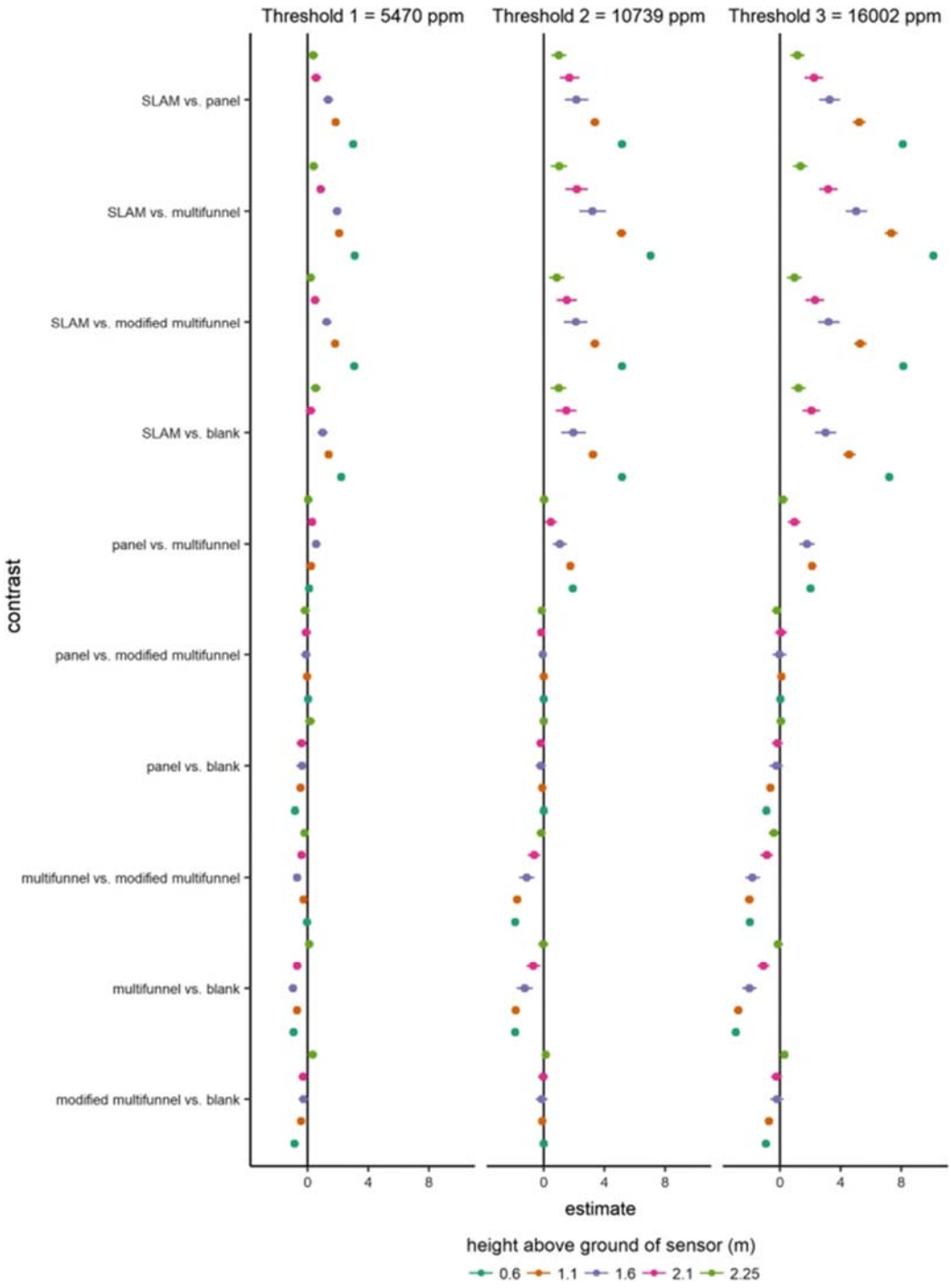

Fig. 5. Results of Tukey's highly significant difference test comparing the mean time to reach a threshold concentration of CO_2 in different insect traps for three different thresholds (columns). Pairwise comparisons are shown on the *y*-axis, the *x*-axis shows the difference in estimated means (± 95% confidence interval) between the two traps. Colors indicate the height above ground of the sensor when the CO_2 readings were taken. Points that intersect the vertical line indicate estimated means that are not significantly different. The horizontal difference between the vertical line and a given point indicates the magnitude of the difference between estimated means; points to the right of a horizontal line indicate the second named trap in a comparison took longer to reach the threshold concentration and points to the left of the line indicate that the second named trap took less time to reach the threshold concentration

Discussion

Optomotor anemotaxis is the process by which insects locate odorant sources (Murlis et al. 1992; Mafra-Neto and Cardé 1994; Farrel et al. 2002; Cardé 2016). This process is influenced by features of the pheromone plume structure including filament frequencies (Baker and Haynes 1989; Murlis et al. 1992). Fluctuations in filament frequencies are mainly introduced into the plume through turbulence (Willis et al. 1994; Cardé 2016). Turbulent dispersion caused by changes in wind speed is the dominant force structuring odor plumes as they move downwind (Murlis et al. 1992), and turbulence causes odorants to disperse into a plume composed of odor filaments interspersed with pockets of clean air (Murlis and Jones 1981; Murlis et al. 2000). The odor plume dispersion is dependent on atmospheric turbulence that may vary in different environments and times during the day (Thistle et al. 2011). The level of turbulence impacts on the probability that insects contact the odor plume because the plume disperses over wider areas at higher levels of turbulence (Thistle et al. 2004).

We observed a large degree of turbulence downwind of the intercept traps, evident in variations in CO_2 burst frequency and intensity levels that declined exponentially with distance from the source (Supplemental Fig. S16). Intermittency, the proportion of time when there is not a signal, is influenced by turbulence in the odor plume and is important for sustained upwind flight in insects (Mafra-Neto and Cardé 1994; Vickers and Baker 1994; but see Justus and Cardé 2002). Some studies have demonstrated that intercept traps introduce turbulence into odor plumes emanating downwind from them and that this turbulence can have important consequences for trap performance (Wyatt et al. 1993; Willis et al. 1994; Geier et al. 1999; Dekker et al. 2001). As an odor plume moves downwind, it expands and the average concentration of odorant within plume boundaries decreases. An insect flying upwind will encounter areas within the plume where the odorant is absent. If these gaps in the plume result in no detection of odorant for about a second or more in male moths, upwind progress ceases (Kuenen and Cardé 1994) and only resumes if the odorant is recontacted. Differences in odor plume structure downwind of different trap designs may be a mechanism that can explain differences in trap capture rate. Similar to Cooperband and Cardé (2006), this study has demonstrated that odorant plume structure differs among different intercept trap designs that differ in their performance for target taxa.

In our study, panel traps captured more insects than multiple-funnel and modified multiple-funnel traps (i.e., captured more *M. scutellatus* and *M. notatus*). This result is generally consistent with the literature on trap design effects on forest insects (Allison and Redak 2017; but see Allison et al. 2014). No differences in the performance of multiple-funnel and modified multiple-funnel traps were observed. The patterns of differences in plume structure we observed downwind of the different trap designs were not consistent with differences observed in the performance of these intercept trap designs. For example, there were differences in the plume structure downwind of the panel and multiple-funnel traps and multiple-funnel and modified multiple-funnel traps, but we observed no differences in the plume structure downwind of panel and modified multiple-funnel traps. These results suggest that differences in plume structure may not explain the differences observed among intercept trap designs in the capture of *M. scutellatus* and *M. notatus*. The generality of this

result for the Cerambycidae depends on how representative *Monochamus* spp. are of longhorned beetles.

It is also possible that our failure to observe patterns in differences in plume structure among the different trap designs consistent with differences in insect captures is an emergent property of limitations of our experimental approach. For example, because of the limitations in the maximum sampling frequency of our infrared spectrophotometer, we were not able to assess vortex shedding frequencies for the different trap designs. Vortex shedding frequencies are predicted to differ for different trap diameters in the same flow environment as they are related to wind speed (0.5 m/s in this study) and the diameter of the object causing turbulence (Sakamoto and Haniu 1990). Another limitation is that our measurements were made sequentially at single locations, and the data from all locations were combined to give an idea of a time averaged 'plume' within the measurement cuboid. Although this approach has been used in other similar studies (Cooperband and Cardé 2006), it does not represent the true instantaneous plume structure because the data were offset in time and space. Thistle et al. (2004) observed that plumes become increasingly less directional from late morning to late afternoon as the boundary layer becomes less stable. Changes in temperature with time of day can result in pockets of air rising (Fares et al. 1980), and vertical movement of plumes has been reported (Schal 1982; Girling et al. 2013). This could have manifested in our experiment if, for instance, there was a net upward drift in the prevailing air movements in the greenhouse. As a result, most plumes would have drifted upward in addition to along the middle of the measurement cuboid, resulting in an altered depiction of the true plume.

Future work should focus on the visualization and modeling of an instantaneous plume downwind of flight intercept traps (e.g., Elkinton et al. 1984; Fares et al. 1980; Strand et al. 2009). The visualization of odor plume structure in a laminar wind tunnel environment can be used to estimate the level of turbulence that different trap designs introduce in the laminar airflow. This approach will require many sensors spread out across the desired measurement area that simultaneously measure the instantaneous concentration of odor plumes downwind of odorant-baited intercept traps at a sufficient frequency of sampling so that vortex shedding frequencies can be calculated. A complementary approach to high-frequency, simultaneous sampling of odor plumes from traps would be to examine how insects perceive variation in plume concentration emitted from flight intercept traps using EAG measurements (Baker and Haynes 1989; Vickers 2006). One technique that shows potential is a mobile EAG that can measure differences in plumes created downwind of different trap designs, and it may provide valuable information on how different odor plumes are detected by insects.

Authors contributions

MCB, JDA and OJG conceived the ideas and designed the methodology; MCB, JDA and CJKM performed data analysis; BS reviewed and edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

Reginald Nott is thanked for technical support. We thank Patt Ross for access to New North Greenhouses, Brian Strom and Ring Cardé for review of an earlier draft and the National Research Foundation of South Africa (Grant #99644), Natural Resources Canada and USDA—Animal and Plant Health Inspection Service (Grant #15–8130-0395-CA), for financial support.

Data accessibility

All data and R code are available on the Dryad Digital Repository (Bouwer et al. 2019).

References

Allison JD, Redak RA (2017) The impact of trap type and design features on survey and detection of bark and woodboring beetles and their associates: a review and meta-analysis. Annu Rev Entomol 62(1):127–146. https://doi.org/10.1146/annurev-ento-010715-023516

Allison JD, Borden JH, Seybold SJ (2004) A review of the chemical ecology of the Cerambycidae (Coleoptera). Chemoecology 14(4):123–150. https://doi.org/10.1007/s00049-004-0277-1

Allison JD, Johnson CW, Meeker JR, Strom BL, Butler SM (2011) Effect of aerosol surface lubricants on the abundance and richness of selected forest insects captured in multiple-funnel and panel traps. J Econ Entomol 104(4):1258–1264. https://doi.org/10.1603/EC11044

Allison JD, McKenney JL, Millar JG, McElfresh JS, Mitchell RF, Hanks LM (2012) Response of the woodborers *Monochamus carolinensis* and *Monochamus titillator* (Coleoptera: Cerambycidae) to known cerambycid pheromones in the presence and absence of the host plant volatile α-pinene. Environ Entomol 41(6):1587–1596. https://doi.org/10.1603/EN12185

Allison JD, Bhandari BD, McKenney JL, Millar JG (2014) Design factors that influence the performance of flight intercept traps for the capture of longhorned beetles (Coleoptera: Cerambycidae) from the subfamilies Lamiinae and Cerambycinae. PLoS ONE 9(3):e93203. https://doi.org/10.1371/journal.pone.0093203

Allison JD, Graham EE, Poland TM, Strom BL (2016) Dilution of fluon before trap surface treatment has no effect on Longhorned Beetle (Coleoptera: Cerambycidae) captures. J Econ Entomol 109(3):1215–1219. https://doi.org/10.1093/jee/tow081

Allison JD, Strom B, Sweeney J, Mayo P (2018) Trap deployment along linear transects perpendicular to forest edges: impact on capture of longhorned beetles (Coleoptera: Cerambycidae). J Pest Sci 92:299–308. https://doi.org/10.1007/s10340-018-1008-7

Baker TC, Haynes KF (1989) Field and laboratory electroantennographic measurements of pheromone plume structure correlated with oriental fruit moth behaviour. Physiol Entomol 14(1):1–12. https://doi.org/10.1111/j.1365-3032.1989.tb00931.x

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc Ser B 57(1):289–300

Bouwer MC, MacQuarrie CJK, Gil OJ, Slippers B, Allison JD (2019) Data from: impact of intercept trap type on plume structure: a potential mechanism for differential performance of intercept trap designs for longhorned beetles. Dryad Digital Repository

Cardé RT (2016) Moth navigation along pheromone plumes. In: Allison JD, Cardé RT (eds) Pheromone communication in moths, 1st edn. University of California Press, California, pp 173–189

Chénier JVR, Philogene BJR (1989) Evaluation of three trap designs for the capture of conifer-feeding beetles and other forest Coleoptera. Can Entomol 121(2):159–167. https://doi.org/10.4039/Ent121159-2

Cooperband MF, Cardé RT (2006) Comparison of plume structures of carbon dioxide emitted from different mosquito traps. Med Vet Entomol 20(1):1–10. https://doi.org/10.1111/j.1365-2915.2006.00614.x

Czokaljo D, Ross D, Kirsch P (2001) Intercept™ panel trap, a novel trap for monitoring forest Coleoptera. J For Sci 47(2):63–65

de Groot P, Nott RW (2001) Evaluation of traps of six different designs to capture pine sawyer beetles (Coleoptera: Cerambycidae). Agric For Entomol 3(2):107–111. https://doi.org/10.1046/j.1461-9563.2001.00087.x

de Groot P, Nott RW (2003) Response of *Monochamus* (Col., Cerambycidae) and some Buprestidae to flight intercept traps. J Appl Entomol 127(9–10):548–552. https://doi.org/10.1046/j.1439-0418.2003.00799.x

Dekker T, Takken W, Cardé R (2001) Structure of host odour plumes influences catch of *Anopheles gambiae s.s.* and *Aedes aegypti* in a dual choice olfactometer. Physiol Entomol 26(2):124–134. https://doi.org/10.1046/j.1365-3032.2001.00225.x

Dodds KJ, Allison JD, Miller DR, Hanavan RP, Sweeney J (2015) Considering species richness and rarity when selecting optimal survey traps: Comparisons of semiochemical baited flight intercept traps for Cerambycidae in eastern North America. Agric For Entomol 17(1):36–47. https://doi.org/10.1111/afe.12078

Elkinton JS, Cardé RT, Mason CJ (1984) Evaluation of time-averaged dispersion models for estimating pheromone concentration in a deciduous forest. J Chem Ecol 10(7):1081–1108. https://doi.org/10.1007/BF00987515

Fares Y, Sharpe PJH, Magnuson CE (1980) Pheromone dispersion in forests. J Theor Biol 84(2):335–359. https://doi.org/10.1016/S0022-5193(80)80010-5

Farrel JA, Murlis J, Long XZ, Li WEI, Cardé RT (2002) Filament-based atmospheric dispersion model to achieve short time-scale structure of odor plumes. Environ Fluid Mech 2(1):143–169. https://doi.org/10.1023/A:1016283702837

Garcia R, Benet M, Arnau C, Cobo E (2004) Efficiency of the cross-over design: an empirical estimation. Stat Med 23(24):3773–3780. https://doi.org/10.1002/sim.2072

Geier M, Bosch OJ, Boeckh J (1999) Influence of odour plume structure on upwind flight of mosquitoes towards hosts. J Exp Biol 202(12):1639–1648. https://doi.org/10.1242/jeb.055186

Girling RD, Higbee BS, Cardé RT (2013) The plume also rises: trajectories of pheromone plumes issuing from point sources in an orchard canopy at night. J Chem Ecol 39(9):1150–1160. https://doi.org/10.1007/s10886-013-0341-9

Justus KA, Cardé RT (2002) Flight behaviour of males of two moths, *Cadra cautella* and *Pectinophora gossypiella*, in homogeneous clouds of pheromone. Physiol Entomol 27(1):67–75. https://doi.org/10.1046/j.1365-3032.2002.00270.x

Kuenen LPS, Cardé RT (1994) Strategies for recontacting a lost pheromone plume: casting and upwind flight in the male gypsy moth. Physiol Entomol 19(1):15–29. https://doi.org/10.1111/j.1365-3032.1994.tb01069.x

Lenth R (2018) Emmeans: estimated marginal means, aka least-squares means. R Package Version 1(2):1

Lewis T, Macaulay EDM (1976) Design and elevation of sex-attractant traps for pea moth, *Cydia nigricana* (Steph.) and the effect of plume shape on catches. Ecol Entomol 1(3):175–187

Lindgren BS (1983) A multiple funnel trap for scolytid beetles (Coleoptera). Can Entomol 115(3):299–302. https://doi.org/10.4039/Ent115299-3

Lingafelter SW (2007) Illustrated key to the longhorned woodboring beetles of the Eastern United States. Coleopterists Society, North Potomac

Mafra-Neto A, Cardé RT (1994) Fine-scale structure of pheromone plumes modulates upwind orientation of flying moths. Nature 369(6476):142–144

McCune B, Grace J (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach

McIntosh RL, Katinic PJ, Allison JD, Borden JH, Downey DL (2001) Comparative efficacy of five types of trap for woodborers in the cerambycidae, buprestidae and siricidae. Agric For Entomol 3(2):113–120. https://doi.org/10.1046/j.1461-9563.2001.00095.x

Miller DR, Crowe CM, Barnes BF, Gandhi KJK, Duerr DA (2013) Attaching lures to multiple-funnel traps targeting saproxylic beetles (Coleoptera) in pine stands: inside or outside funnels? J Econ Entomol 106(1):206–214. https://doi.org/10.1603/EC12254

Morewood WD, Hein KE, Katinic PJ, Borden JH (2002) An improved trap for large wood-boring insects, with special reference to *Monochamus scutellatus* (Coleoptera: Cerambycidae). Can J For Res 32(3):519–525. https://doi.org/10.1139/x01-224

Murlis J, Jones C (1981) Fine-scale structure of odour plumes in relation to insect orientation to distant pheromone and other attractant sources. Physiol Entomol 6(1):71–86. https://doi.org/10.1111/j.1365-3032.1981.tb00262.x

Murlis J, Elkinton JS, Cardé RT (1992) Odor plumes and how insects use them. Annu Rev Entomol 37(1):505–532. https://doi.org/10.1146/annurev.en.37.010192.002445

Murlis J, Willis MA, Cardé RT (2000) Spatial and temporal structures of pheromone plumes in fields and forests. Physiol Entomol 25(3):211–222. https://doi.org/10.1046/j.1365-3032.2000.00176.x

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, New York

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2020). nlme: linear and nonlinear mixed effects models. R package version 3.1-144. https://CRAN.R-project.org/package=nlme

R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Sakamoto H, Haniu H (1990) A study on vortex shedding from spheres in a uniform flow. J Fluid Eng 112(4):386–392. https://doi.org/10.1115/1.2909415

Schal C (1982) Intraspecific vertical stratification as a mate-finding mechanism in tropical cockroaches. Science 215(4538):1405–1407. https://doi.org/10.1126/science.215.4538.1405

Strand T, Lamb B, Thistle H, Allwine E, Peterson H (2009) A simple model for simulation of insect pheromone dispersion within forest canopies. Ecol Model 220(5):640–656. https://doi.org/10.1016/j.ecolmodel.2008.11.018

Thistle HW, Peterson H, Allwine G, Lamb B, Strand T, Holsten EH, Shea PJ (2004) Surrogate pheromone plumes in three forest trunk spaces: composite statistics and case studies. For Sci 50(5):610–625. https://doi.org/10.1093/forestscience/50.5.610

Thistle H, Strom B, Strand T et al (2011) Atmospheric dispersion from a point source in four southern pine thinning scenarios: basic relationships and case studies. Trans ASABE 54:1219–1236. https://doi.org/10.13031/2013.39021

Tukey JW (1949) Comparing individual means in the analysis of variance. Biometrics 5(2):99–114. https://doi.org/10.2307/3001913

Ulyshen MD, Sheehan TN (2019) Trap height considerations for detecting two economically important forest beetle guilds in southeastern US forests. J Pest Sci 92:253–265. https://doi.org/10.1007/s10340-017-0883-7

Vickers NJ (2006) Winging it: moth flight behavior and responses of olfactory neurons are shaped by pheromone plume dynamics. Chem Senses 31(2):155–166. https://doi.org/10.1093/chemse/bjj011

Vickers NJ, Baker TC (1994) Reiterative responses to single strands of odor promote sustained upwind flight and odor source location by moths. Neurobiology 91(13):5756–5760. https://doi.org/10.1073/pnas.91.13.5756

Willis MA, Murlis J, Cardé RT (1994) Effects of pheromone plume structure and visual stimuli on the pheromone-modulated upwind flight of male gypsy moths (*Lymantria dispar*) in a Forest. J Insect Behav. https://doi.org/10.1007/BF01989742

Wyatt TD, Phillips ADG, Gregoire JC (1993) Turbulence, trees and semiochemicals: wind-tunnel orientation of the predator, *Rhizophagus grandis*, to its barkbeetle prey *Dendroctonus micans*. Physiol Entomol 18(2):204–210. https://doi.org/10.1111/j.1365-3032.1993.tb00469.x

Wyatt TD, Vastiau K, Birch MC (1997) Orientation of flying male *Anobium punctatum* (Coleoptera: Anobiidae) to sex pheromone: separating effects of visual stimuli and physical barriers to wind. Physiol Entomol 22(2):191–196. https://doi.org/10.1111/j.1365-3032.1997.tb01157.x

Yanega DN, Natural History Survey Division (1996) Field guide to northeastern longhorned beetles (Coleoptera:Cerambycidae). Illinois Natural History Survey, Champaign

Yaws CL (2014) Diffusion coefficient in air—organic compounds. In: Yaws CL (ed) Transport properties of chemicals and hydrocarbons, 2nd edn. Gulf Professional Publishing, Oxford, pp 407–496

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York. https://doi.org/10.1007/978-0-387-87458-6