

Three-Dimensional Orientation of Male *Cadra cautella* (Lepidoptera: Pyralidae) Flying to Calling Females in a Windless Environment

R. W. MANKIN¹ AND D. W. HAGSTRUM²

Environ. Entomol. 24(6): 1616–1626 (1995)

ABSTRACT A male *Cadra cautella* (Walker) flying in a windless environment first reacts behaviorally to the sex pheromone plume of a calling female from a distance of ≈ 40 cm. Its angular velocity (turning rate in degrees per second) increases and, if it approaches within ≈ 20 cm, its velocity decreases gradually until it lands near the female. The orientation pattern differs from orientation in wind primarily in the fraction of turns with net movement away from the female, initially ≈ 0.5 . This fraction decreases to ≈ 0.2 if the male approaches within ≈ 10 cm. Previously developed computer models suggest that such behavior is less efficient for finding a pheromone source than pheromone-stimulated optomotor anemotaxis but more efficient than random searching. Thus, it can be expected that pheromone traps are less effective at sampling remote populations of insects in a warehouse than in a field, but are helpful in pinpointing nearby infestations.

KEY WORDS stored product moths, searching behavior, sex pheromone, communication

AN INSECT IN SEARCH OF a mate quickly modifies its flight behavior when it detects sex pheromone. Information it perceives through olfaction, vision, and mechanoreception triggers changes in velocity and angular velocity (degrees per second) that direct its motion toward the pheromone source. The motion is strongly affected by the concentration, shape, and structure of the pheromone plume (for example, Cardé and Hagaman 1979, Payne et al., 1986, Vickers and Baker 1992, Charlton et al. 1993), all of which are modulated by dynamic changes in wind turbulence, velocity, and direction (for example, Gibson and Brady 1985, Willis and Arbas 1991, Liu and Haynes 1993). The mechanisms of searching behavior are now understood sufficiently to enable some control of the insect's turning frequency and speed in a wind tunnel by presenting it with short, precisely timed pheromone pulses (Mafra-Neto and Cardé 1994, Vickers and Baker 1994).

Much of the research on pheromone-stimulated searching behavior has focused on the typical case where the insect is flying in wind; nevertheless, the mechanisms by which insects find pheromone sources in the absence of wind are of practical and ethological concern. Pheromone traps are commonly used in warehouses to pinpoint infestations of stored product insects. Experimental modifications of trap locations, sizes, shapes, and emission sources have enabled improvements in trap utility

(Burkholder and Ma 1985, Vick et al. 1990), but further improvements would accrue from a better understanding of searching behavior in these environments.

Literature concerning orientation without wind is scattered through many different research areas. A large group of studies deals with orientation to resources (foraging) without directional cues. Historically, orientation without directional cues was described as orthokinesis, klinokinesis, or klinotaxis. In recent years, strict definitions of these terms have been difficult to maintain as more examples have been described (for example, Bell and Tobin 1982). Stinner and Bachelor (1993) reviewed the literature on foraging and derived a search model that has applicability to mate-seeking behavior either with or without wind. In their model, search near a resource is a spiral with a high angular velocity and low velocity. A gradual transition to low angular velocity and higher velocity occurs away from the resource.

Other studies consider orientation without wind as a case of reduced orientational information. Bell and Tobin (1982) described the general case. Baker and Kuenen (1982), Kuenen and Baker (1982), and Baker et al. (1984) analyzed the behavior of male *Grapholita molesta* (Busk) under different wind conditions (steady, ceasing, zero wind), with and without pheromone. David and Kennedy (1987) compared flight by *Lymantria dispar* (L.) with and without wind and pheromone. Willis and Cardé (1990) analyzed *L. dispar* flights at several wind speeds including zero. In all these studies, the angles between zigzags (turn magnitudes) were

¹ Insect Attractants, Behavior, and Basic Biology Research Laboratory, USDA-ARS, Gainesville, FL 32604.

² U.S. Grain Marketing Research Laboratory, USDA-ARS, Manhattan, KS 66502.

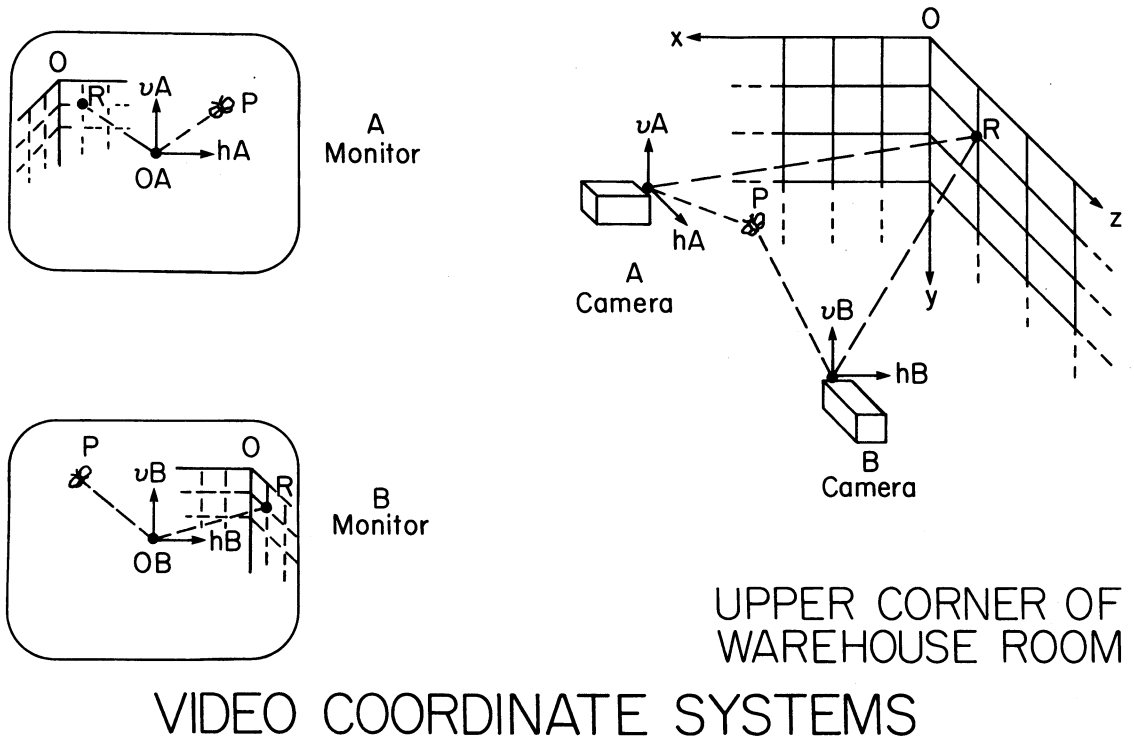


Fig. 1. Coordinate systems used for position, P, of a moth flying in a warehouse room and the positions of the moth on the monitors of cameras A and B recording the flight. O, OA, and OB are, respectively, the origins in the room, A-camera, and B-camera coordinate systems. R is a fixed reference point on 1 wall. In the room coordinate system, y is the vertical axis; x and z are horizontal axes. In the monitor coordinate systems, v_A and v_B are the vertical axes, and h_A and h_B are the horizontal axes for the A and B monitors, respectively.

greater without than with wind. Velocity decreased as windspeed decreased, but at zero windspeed it increased. Turning frequency was unaffected by changes in windspeed. The fraction of turns downwind (that is, turn bias away from female) increased when wind decreased to zero. On average, moths could orient without wind to pheromone sources but their efficiency was reduced.

Several studies have examined mate location by stored product moths in a warehouse environment (Hagstrum and Davis 1980, 1982; Mankin et al. 1983). The instantaneous wind velocity in a warehouse is not necessarily zero even if the building is airtight and the temperature is uniform. However, orientational cues are much reduced compared with those in the field and in wind-tunnel experiments cited above. The warehouse studies focused on coarse-scale flight patterns (movement among 1.4-m cubes), but it was observed that flights by *Cadra cautella* (Walker) and *Plodia interpunctella* (Hübner) males became area restricted (that is, net movement decreased) near a pheromone source. For male *C. cautella*, area-restricted flight began at distances <60 cm from the female. This distance decreased in a pheromone-permeated atmosphere.

To gain more insight into the mechanisms of orientation to pheromone in a windless environment,

and to characterize male *C. cautella* area-restricted flight precisely, we conducted a detailed, 3-D video analysis of searching behavior with and without calling females in a warehouse room.

Materials and Methods

Arena. Flights were observed inside an interior room (5.9 by 5.9 by 5.9-m) of a warehouse described previously in Hagstrum and Davis (1980) and Mankin et al. (1983). The north and east walls of the upper northeast corner had been gridded in lines 10-cm apart (Fig. 1). Light was provided by sixteen 40-W fluorescent bulbs paired at 8 evenly spaced locations on the ceiling. The translucent covers beneath the light fixtures were covered by Plexiglas barriers. Wind currents were negligible during tests because of the arena's interior location, remote from sources of wind drafts or temperature differentials. Periodic checks with a hot-wire anemometer (ThermoSystems model 1610-12, St. Paul, MN) typically found velocities of 2–5 cm/s, the same order of magnitude as the thermal currents generated by the hot-wire itself. Temperatures during the tests were 24–28°C.

Two surveillance cameras (Panasonic model 1050A, Matsushita Electric, New York) were con-

nected to separate time-lapse videotape recorders and observed from monitors (Panasonic model 8030 and TR195B, respectively). They were pointed perpendicular to each other and toward the ceiling at the northeast corner of the room. Specifically, camera A faced east, 440 cm from the east wall, 10 cm below the ceiling, and 60 cm from the north wall (XA, YA, ZA = 440, 10, 60 cm in room coordinates). Camera B faced north from (XB, YB, ZB = 60, 10, 440 cm). Digital timers (0.1-s resolution) were set near the walls in both fields of view to enable synchronization of the frames recorded from the 2 cameras. The total space in the combined fields of view was approximately the same volume contained in the 1.4-m cubes used in an earlier study of *C. cautella* searching behavior in the entire warehouse room (Hagstrum and Davis 1980).

Insects. *C. cautella* was reared and handled as described in Hagstrum and Davis (1980) (a photoperiod of 14:10 [L:D] h, with observations beginning at the start of scotophase at 1400 hours). Unmated adults were collected in the morning of the previous day and placed in separate vials. A female, when present, was strapped before testing on the ceiling inside a petri dish at FEMREFPT (female reference point = 50, 0, 50 cm) in the room coordinate system. The dish was removed just before males were released in the center of the floor. If a male ceased flying, another was released, up to a total of 4. The place where a female settled and called, FEMCALLPT, was usually within ≈ 10 cm. The reference origin for calculation of distances and angles was FEMCALLPT when a female was present, and FEMREFPT otherwise.

Flight Analysis. Moth flights in the field of view of both cameras were digitized from the monitor screen with a digitizer (Numonics model 1220, Lansdale, PA) and converted to 3-D room coordinates by subroutines (Mankin et al. 1987) operating on a microcomputer (Digital Equipment model PDP 11/23, Maynard, MA). The recordings were replayed and digitized, frame by frame. The digitizer sent the moth's coordinates to a printer or a datalogger (Campbell Model CR20, Logan, UT), which stored them on a digital cassette recorder. The data on the cassette recorder were transmitted to the microcomputer for analysis.

A customized program containing ≈ 80 user-written and 50 vendor-supplied (DEC-graphics) subroutines calculated the moth's room coordinates from the digitized monitor images. The functions done by the software included file retrieval from the digitizer station, timing synchronization between files recorded from different cameras, translation of files into binary format, 3-D reconstruction of the flight from the monitor coordinates, and 3-D motion analyses of individual flights. Part of the retrieval program was written in assembly language. The remainder of the programming was in FORTRAN IV.

The calculation of 3-D position from 2 cameras is described elsewhere (for example, Rogers and Adams 1976, and Longuet-Higgins 1981). The algorithm used in this report is given in *Appendix 1*.

Calibration and Error Reduction. Several procedures were instituted to reduce digitization and synchronization errors. Digitizer errors were minimized by averaging 6 consecutive frames (1/60-s intervals) to construct data sets of average x, y, and z coordinates in 0.1-s intervals (*Appendix 1*). To determine the precision of the digitizer-microcomputer system, the screen coordinates of 4 points (grid intersections) on the east wall were digitized and stored at the beginning of each flight file. The positions of 3 points were predicted from calculations based on the 4th point. These were compared with the actual positions in 2 separate recordings. The discrepancy between the predicted and actual position of a grid intersection increased with its distance from the reference point up to 4 cm for points at the edge of the screen. To reduce calibration error, the orientation reference chosen for each flight was the measured intersection closest to the moth initial position.

Statistical Analysis. Nineteen flights of individual males and 8 flights of males that found females were stored as SAS data files (SAS Institute 1985) of average x, y, and z coordinates in 0.1-s intervals. The distance between male and female, velocity, and angular velocity were calculated by the algorithm described in *Appendix 2*. Turn bias was calculated by subtracting the distance between male and female from that in the previous interval, setting the bias for distances < 0 to 0 and > 0 to 1, and averaging over each cm distance from the female.

Equations were fit to mean velocity, angular velocity, and turn bias as a function of distance from female (DISTFEM) using PROC REG and PROC NLIN procedures (SAS Institute 1985). One-tailed *t*-tests were applied to the standard errors of the predicted values to find the distances at which slopes were significantly different from zero and the distances at which motion parameters were significantly affected by a calling female.

For comparisons with other studies of searching behavior in wind, a second data set was constructed by approximating each flight as a series of straight tracks between turns $> 45^\circ$. Turn magnitude (TurnMag) was calculated as the angle between 2 consecutive straight tracks. An estimate of track angle (TrkAngle) was calculated as the supplement of the heading (Akers 1989); that is, the angle between the straight track and the line pointing to the reference origin. Note, however, that the actual track angle (Marsh et al. 1978) is undefined in zero wind. Length of straight track was calculated as the distance between 2 consecutive turns. Interturn interval was the time between 2 consecutive turns. The interturn intervals, lengths, track angles, and turn magnitudes were compared at dif-

