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RADAR OBSERVATIONS OF ORIENTATION OF NOCTUIDS MIGRATING FROM CORN FIELDS IN THE LOWER RIO GRANDE VALLEY

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ABSTRACT

This paper describes measurements of orientation behavior of insects migrating from corn fields located in the Lower Rio Grande Valley of northeastern Mexico and south Texas. Radar, biological, and meteorological data were collected during May and June of 1985 to 1990. The two species of Noctuidae (Lepidoptera) that dominated the radar echoes were corn earworm, *Helicoverpa zea* (Boddie), and fall armyworm, *Spodoptera frugiperda* (J.E. Smith). Common alignment of the insects' body axes occurred during each night (n = 84). Crab angles (difference between insect alignment and wind displacement direction) were 30° or greater during 85% of those nights when alignment occurred for more than 1 hr, and aligned insects occurred within a layer 200 m or greater in thickness. Alignment was perpendicular to the wind direction when the wind was from the SE. Minimum and maximum fallout areas were simulated by assuming various flight behaviors. These simulations indicate that collective orientation changes the mean displacement of migrants with respect to wind displacement and decreases fallout area when compared with random orientation. A smaller fallout area implies a greater concentration of migrants in the fallout area. Thus, collective orientation can impact agricultural production and gene mixing. Also, significance of orientation behavior varies inversely with wind speed and size of source area.

INTRODUCTION

Raulston et al. (1992) estimated that as many as seven billion corn earworm, *Helicoverpa zea* (Boddie), adults may develop on corn grown in the Lower Rio Grande Valley (LRGV) of

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Texas and northeastern Mexico in one season. Most adults emerge as the crop matures during late May and early June when prevailing winds are from the SE. These winds provide a mechanism for transporting moths from the source area to new habitats and toward the low level wind jets reported by Bonner (1968).

A ground-based radar detected large numbers of moths departing the corn fields (Wolf et al. 1994). Each night, the departure started approximately 30 minutes after sunset, and the moths quickly merged into a "cloud" that passed over the radar. Wolf et al. (1990) used an airborne radar for detecting the edge of an insect cloud departing the LRGV. Successive detection of the cloud edge indicated that it moved at least 400 km in one night (7.7 hours). Active flight of the insects and the wind affected the displacement of the insect cloud.

The contribution of active flight to displacement depends upon the insect's airspeed, orientation, and flight duration. W. W. Wolf (unpublished data) used a police radar gun to measure the airspeed of a free-flying *H. zea* moth at 5 m/s. However, Westbrook et al. (1994) reported a mean airspeed of 4.5 m/s for *H. zea* sized moths. At this speed, the potential distance contributed by active flight would be 162 km for a flight lasting 10 hours. Lingren et al. (1995) obtained a slightly lower mean airspeed of 3.5 m/s for *H. zea* moths.

Orientation of night-flying insects toward the direction of wind displacement was reported by Drake et al. (1981), Drake (1985), Riley and Reynolds (1986), and Greenbank et al. (1980). It is not always clear whether reports of "down-wind flight" refer to the apparent displacement across the ground or the actual insect orientation (Brown 1970). Reports of insects orienting perpendicular to the wind direction are rare - especially when wind speed exceeds insect airspeed.

This paper reports the orientation of adult noctuid insects emigrating from corn fields in the LRGV and simulates some consequences of this behavior.

MATERIALS AND METHODS

Definitions used in this manuscript include

(a) orientation = compass direction in which the head of an insect points,

(b) alignment = mean compass direction of the longitudinal axes of a group of insects,

(c) crab angle = difference between wind direction and insect alignment,

(d) insect airspeed = speed of the insect with respect to the air as distinguished from its speed with respect to the earth,

(e) Tterm = time of migration termination,

(f) Tmig = duration of migration from flight initiation until Tterm,

(g) Wdist = mean distance of wind displacement with respect to ground during Tmig,

(h) Mdist = mean distance traveled by migrants with respect to the air during Tmig,

(I) drift = mean location of migrants with respect to wind displacement at Tterm, and

(j) Rfa = ratio of fallout area of migrants to source area (undefined for a point source).

Radar Observations. Airborne insect alignment was measured with a ground-based X-band, Decca Marine radar. The radar antenna consisted of a 1.2 m diameter parabolic reflector that rotated 360° in azimuth every 3 s. The radar could detect an individual *H. zea* sized moth to a distance of 2.2 km. Locations of individual moths were displayed as bright dots on a plan position indicator (PPI). Movie filming (16 mm) of the PPI provided time-lapse sequences of insect alignment and movement. Each movie frame represented one revolution of the radar antenna.

The radar was located 13 km south of Donna, TX (26.06°N, 97.97°W), within 100 m of the north bank of the Rio Grande River. This location was centered at the prevailing down-wind edge of the largest irrigated corn production region in Mexico (Anonymous 1983). Growers plant about 200,000 ha of corn annually in this region. Radar observations of moth flight activity were made for 84 nights during late May and early June, 1985 through 1990. These observations provided data on insect alignment, flight altitude, and insect concentration in the atmosphere.

Insect alignment is determined from the patterns of bright dots displayed on the PPI screen (Schaefer 1976). When the insects are randomly oriented, a circular pattern appears on the PPI screen. In contrast, orientation of insects in a common direction results in a "dumbbell" shaped pattern. The axis of a "dumbbell" pattern on the PPI screen is perpendicular to the mean alignment of the longitudinal axes of all the insects detected during each antenna revolution. Only the mean alignment of the insects' longitudinal axes is apparent (Riley and Reynolds 1986). Cephalic and caudal ends are indistinguishable because the insects and "dumbbell" lobes are symmetrical. Therefore, actual insect orientation is ambiguous by ±180°. For example, an alignment measurement of 90° includes insects orienting toward 90° or the diametrical direction of 270°.

Measurements at nine altitudes, from 68 to 1200 m above ground level (AGL), provided a vertical profile of insect alignment (Wolf et al. 1986). Each profile required 5 to 10 min of time. Profiles were measured at 10- to 15-min intervals while insect concentrations increased, and at 30- to 60-min intervals after concentrations decreased by one half. Each measurement of insect alignment represented the mean alignment of all insects detected during at least five revolutions of the antenna (15 s).

Meteorological Observations. Air temperature, relative humidity, and barometric pressure were measured at 1.5 m AGL with a Campbell Scientific weather station, model CR21. Wind speed and direction were measured at 3 m AGL. Also, vertical profiles of wind velocity were obtained by using a theodolite for tracking helium filled balloons. Balloon tracking began at sundown and continued at approximately 1-h intervals. The balloon launched within one hour after sunset was instrumented to report upper-air temperature, wet-bulb temperature, and barometric pressure (Westbrook et al. 1995).

Entomological Observations. Estimates of *H. zea* and *S. frugiperda* populations developing in corn were obtained using the soil sampling methods of Raulston et al. (1992). All developmental stages of both species occurring in the soil (prepupae, pupae, and exuviae) were excavated from two, 1 m^2 samples from each of 90 to 120 fields each year. Also, infestation levels in the fields were determined by recording damage caused by larvae, live larvae in the primary ear, and larval cut-outs from 50 plants in each field (25 consecutive plants on each side of the 1 m^2 soil sample).

Data Analysis. Total number of *H. zea* and *S. frugiperda* adults that developed on the corn crop was estimated by multiplying area densities of pupae from soil samples (number per ha) times the average hectares of corn.

Wind speed and direction data were interpolated to 100 m altitude intervals and plotted on the same graph as insect alignment. Statistical comparisons of wind direction and alignment data (for the same time and altitude) required two additional interpolations. Therefore, interpolated 100 m winds were linearly interpolated to the time of radar measurements, and radar data were linearly interpolated to 100 m altitude intervals. Data were classed by time after sunset, wind direction, and wind speed. Frequency of occurrence of common alignment included only observations when insect concentration was greater than 0.2 insects per million cubic meters.

Crab angles included the interval -90° to +90° because alignment was ambiguous by ±180°. A crab angle of 0° or 90° indicates alignment parallel or perpendicular to the wind, respectively. Also, positive or negative crab angles indicate alignment clockwise or counterclockwise of the wind direction, respectively. A non-zero crab angle results in insect drift to the left or right of wind displacement. Drift was determined from time-lapse film. Criteria for selecting film sequences were (a) adequate duration of each sequence, (b) upper wind measurements within 1-h of the film sequence, (c) weak winds (0-4 m/s), and (d) moderate winds (8-12 m/s). Film sequences were grouped by 2 hr increments and evaluated for right, left, or undetermined drift with respect to the wind. The undetermined class included records where the ratio of wind-speed to insect-airspeed, crab angle, or insect concentration prevented left or right classification.

Means and 95% confidence limits of angular data were obtained using circular statistics (Batschelet 1981). The algorithms required axial data (insect alignments and crab angles) to be multiplied by two. Alignment was recorded to the nearest 5°; therefore, no correction for grouping was necessary. Test criteria for comparisons between two means of angular data were based on separation of upper and lower confidence limits. Means of frequency-of-occurrence of alignment were compared using least significant differences.

Consequences of Orientation. We simulated consequences of insect orientation by calculating mean insect drift and fallout area. Minimum and maximum consequences were obtained by assuming extreme insect flight behaviors. These extreme behaviors were (a) collective orientation toward a single direction, (b) random orientation, (c) zero fallout during Tmig, and (d) constant fallout during Tmig. For each of these behaviors, four additional extreme assumptions were applied: (a) zero variance in orientation (no turning during migration), (b) zero atmospheric dispersion, (c) uniform insect airspeed equal to the maximum airspeed for the species, and (d) zero variation of insect behavior or wind versus altitude. Constant fallout refers to an imaginary behavior with fallout of a constant portion of migrants during arbitrary time intervals between flight initiation and Tterm.

Drift and Rfa were calculated for the following parameters: (a) wind speed = 10 m/s, (b) migration period, Tmig = 10 hr, (c) insect airspeed = 5 m/s, (d) crab angles = 0°, -90°, and 180°, and (e) source diameters = 10 and 100 km.

RESULTS

Entomology. The pupae of *H. zea* and *S. frugiperda* were the largest and most numerous of the species recovered from soil samples. Area densities of recovered pupae ranged from 1.1 to 4.3 per m^2 for *H. zea*, and from 0.2 to 7.6 per m^2 for *S. frugiperda* (Table 1). Our estimates of total number of *H. zea* and *S. frugiperda* adults produced on fruiting corn in the test area ranged from 2.2 to 8.6 billion and 0.4 to 15.2 billion, respectively.

Meteorology. The wind direction from 100 to 200 m altitude at sunset was from the northeast (NE), southeast (SE), southwest

TABLE 1. Annual Variation of Infestation and Area Density of *H. zea* and *S. frugiperda* in Corn Fields in the Lower Rio Grande Valley.

Year	Number of Fields	Percent of fruit Infested	Avg per m^2 of soil *H. zea*	Avg per m^2 of soil *S. f.*[a]	Percent *H. zea*
1985	101	81 (1.3)[b]	3.8 (0.20)	0.2 (0.03)	95
1986	120	94 (0.7)	3.6 (0.20)	2.5 (0.20)	59
1987	105	77 (1.1)	1.1 (0.20)	0.3 (0.04)	79
1988	90	90 (0.8)	3.5 (0.10)	0.2 (0.05)	95
1989	100	98 (0.5)	4.3 (0.20)	7.6 (1.20)	36
1990	100	78 (1.2)	3.2 (0.20)	1.1 (0.10)	74

[a] *S. frugiperda*

[b] Number in parentheses is standard error of the mean. Soil samples included all developmental stages excavated whether dead or alive.

(SW), and northwest (NW) for 14, 83, 1, and 1% of the observation nights (n = 84), respectively (Table 2). Frequencies of occurrence of interpolated wind directions (n = 4,527) were 11, 84, 2.7, and 1.7% from the NE, SE, SW and NW, respectively. The difference in frequency of occurrence of interpolated wind directions compared with wind direction at sunset results from wind shifts during the first 4 hrs after sunset and vertical shear of wind direction. Wind speeds were less than 12, 24, 16, and 10 m/s for winds from the NE, SE, SW, and NW, respectively, for 98% of the observations.

The qualitative relationship between wind direction and insect alignment can be shown graphically (Fig. 1). In this figure, insect alignment and wind velocity are represented by short bars and wind flags, respectively. Wind flags or alignment bars plotted vertically or horizontally designate north-south or east-west directions, respectively. Small circles designate either random or immeasurable insect alignment. Short, long, and triangular wind-flag barbs represent wind speeds of 1, 2, and 10 m/s, respectively. Figures were selected as examples, and do not represent all patterns of alignment and wind direction that were observed.

When SE winds became established for several successive nights, the wind direction was uniform at all altitudes (Fig. 1a). Wind direction shear (change of wind direction) from 100 to 1200 m altitude exceeded 30° during 18% of the nights (Fig. 1b). A counterclockwise temporal and/or vertical shear of wind direction greater than 30° occurred on 11% of the nights (Figs. 1b and 1c). Uniform north winds were rare (<3% of nights Fig. 1d).

TABLE 2. Dates (6 years, 84 Nights) and Wind Directions for Radar and Meteorological Observations in the Lower Rio Grande Valley, Texas.

1985	1986	1987	1988	1989	1990
6/07 SE-1[a]	6/03 SE[b]	5/29 SE	5/29 SE	6/02 SE	5/31 SE
6/08 SE	6/04 SE	5/30 SE	5/30 SE	6/03 SE	6/01 SE
6/10 SE	6/05 SE	6/01 SE	5/31 SE	6/04 SE	6/02 SE
6/11 SE	6/06 SE-2	6/02 SE	6/01 SE	6/05 SE	6/03 SE
6/12 NE-1-2	6/07 SE	6/03 NE-2	6/02 SE-2	6/06 SE	6/04 SE
6/13 NE-1	6/08 SE	6/04 NE-2	6/03 NW-1-2	6/07 SE-2	6/05 SE
6/14 NE	6/12 SE	6/07 NE	6/06 SE-2	6/08 NE	6/06 SE
6/16 NE-1		6/09 SE	6/07 SE-2	6/09 SE	6/07 SE
6/17 SE		6/10 SE-2	6/08 SE-2	6/10 SE	6/09 SE-1
6/18 SE		6/11 SE	6/09 SE-2	6/11 SE	6/11 SE
6/19 NE		6/12 SE	6/10 NE-2	6/12 SE	6/12 SE
6/20 SE-1			6/11 SE	6/13 SE	6/13 SE
6/21 SE			6/12 SE	6/14 NE-2	6/14 SE
6/22 SE			6/14 SE	6/15 NE-2	
6/24 SE			6/15 NE	6/16 SE	
6/25 SE			6/16 SE	6/17 SE	
			6/17 SE	6/18 SE	
				6/19 SE	
				6/20 SE	
				6/21 SE	

[a] Numbers to the right of wind directions designate:

-1 Wind shifted 30° or greater during 1st 4 hours after sunset.

-2 Wind shifted 30° or greater between 100 and 1200 m altitude.

[b] NE, SE, SE and NW designates wind directions from the northeast, southeast, southwest and northwest, respectively, at sunset and between

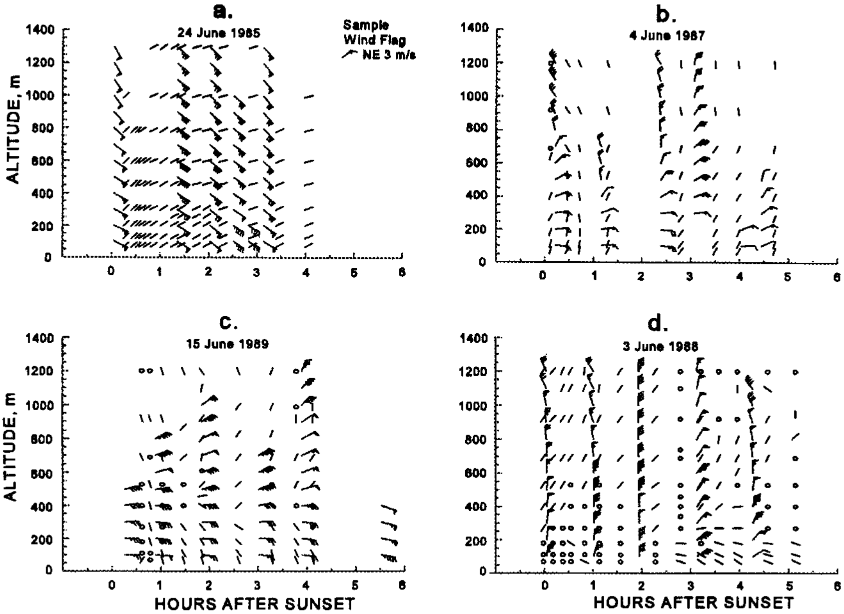

FIG. 1 Examples of the relation between insect alignment (bars) and wind direction (flags) for: (a) frequent SE wind and crosswind alignment; (b) greater than 90° shear above 300 m altitude with parallel and crosswind alignment; (c) change of alignment with wind direction; and (d) uniform north wind with small crab angles.

Radar. We estimated that at least 90% of the insects detected by the radar were *H. zea* and *S. frugiperda*-sized moths. These larger insects dominated insect alignment measurements obtained from the radar screen.

Collective insect alignment was detected during each of the 84 nights. The relation between insect alignment and wind direction shown in Fig. 1a was common. Insect alignment was seldom parallel to the wind direction, and alignment changed as wind direction changed. Insect crab angles of 30° or greater (Fig. 1a) occurred during 85% of those nights when insects were aligned for more than 1 hr, and the vertical depth of the alignment was >200 m. Examples of wind shear that was accompanied by changes in insect alignment are shown in Figs. 1b, 1c, and 1d. Counterclockwise (Figs. 1b and 1c) and clockwise (Fig. 1d) changes of wind direction and insect alignment occurred during different nights.

For wind speeds of 0 to 4 m/s, time-lapse film sequences showed left drift (33%, n = 12) for SE winds and right drift (60%, n = 5) for NW winds (Table 3). For moderate wind speeds of 8 to 12 m/s, the film also showed left drift (22%, n = 32) for SE winds as well as left drift (27%, n = 11) for NE winds.

Subtle influences of wind velocity on insect alignment behavior could not be assessed by visual examination of graphs and time-lapse film. Therefore, the following results used interpolated radar and meteorological data. We assumed that winds within a 90° sector did not affect alignment behavior and sorted the data by NE, SE, SW, and NW wind directions.

TABLE 3. Insect Displacement Relative to Wind Displacement as Indicated by Time-Lapse Movie Film of Radar Display.[a]

Wind Speed	Wind Quadrant	Total Records	Percent of Records with Drift: Left	Right	Unknown
0-4 m/s	NE	6	17	17	67
0-4	SE	12	33	17	50
0-4	SW	3	33	33	33
0-4	NW	5	20	60	20
8-12 m/s	NE	11	27	18	55
8-12	SE	32	22	3	75
8-12	SW	2	0	50	50
8-12	NW	1	0	0	100

[a] Wind direction measured by tracking a helium-filled balloon with radar or theodolite within one hour of movie record.

The axis of average alignment was in the NE-SW quadrants regardless of wind direction (Fig. 2). Histograms of interpolated wind directions, insect alignment, and crab angles for 15° class intervals are also shown in Fig. 2. The confidence interval (±8°, $P < 0.05$) for mean insect alignment was smallest for SE winds; however, this may be an artifact of uniformity of wind direction and the greater number of observations. Mean insect alignment during SW winds was different than alignment during NE, SE, and NW winds. Also, mean alignment was greater for SE than for NW winds. However, alignment was the same for winds from NE and NW or NE and SE.

Large positive and negative crab angles (mean = 89 ± 11°) occurred with winds from the SE (Fig. 2). Small crab angles occurred with NW winds. The greatest confidence interval (±35°, $P < 0.05$) and negative mean crab angle occurred with NE winds. Mean crab angles were positive for SW and NW winds. Crab angles were smaller for NW than for SE winds. Mean crab angles were similar for SE and SW winds and for SW and NW winds.

Insect alignment occurred most frequently with NW winds (Table 4); however, NW winds only occurred during 5 nights.

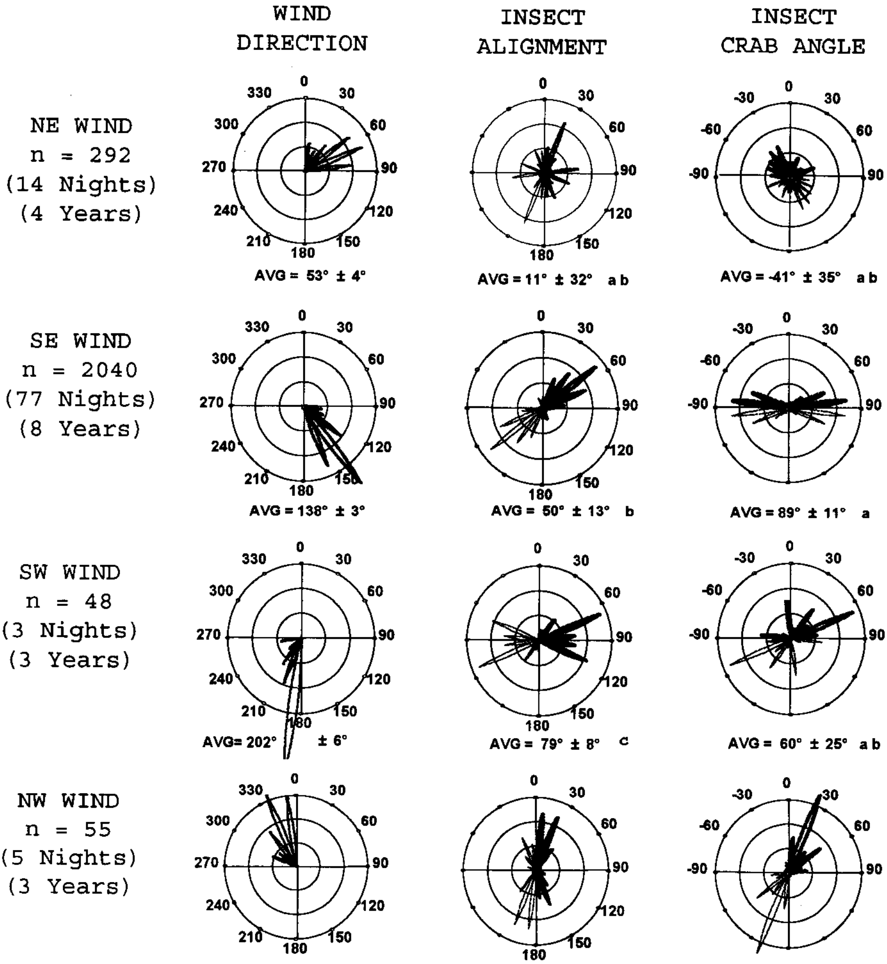

FIG. 2 Histograms of wind direction, insect alignment, and insect crab angles (columns) when winds were from NE, SE, SW or NW (rows). Length of solid lobes represents the percent of observations per 15° class interval. Radial scale is 10% per concentric circle. Axial data (alignment and crab angle) have diametrical lobes drawn with narrow lines. Means within columns followed by the same letter are not significantly different ($P < 0.05$) based on separation of upper and lower confidence limits. Radar measurements made 1-4 hrs after sunset near Donna, TX, 1985-1990.

TABLE 4. Radar Measurements Showing Frequency of Occurrence of Orientation and Total Number of Observations for Several Classes of Wind Direction, Wind Speed and Time after Sunset. Radar Measurements near Donna, TX. 1985-1990.

Wind Speed m/s	Number of Observations with Oriented Insects			Percent of observations with Oriented Insects		
	Early[a]	Late[b]	All[c]	Early	Late	All
			Northeast Wind			
0-04	272	238	510	62	36	50
4-09	286	262	548	50	61	55
9-14	74	98	172	66	58	61
>14	--[d]	--	--	--	--	--
All	632	598	1230	54	51	53
			Southeast Wind			
0-04	86	109	195	65	17	38
4-09	952	872	1824	52	53	52
9-14	1492	867	2359	63	52	59
>14	655	648	1303	57	41	49
All	3185	2496	5681	59	48	54
			Southwest Wind			
0-04	16	33	49	63	30	41
4-09	12	24	36	83	88	86
9-14	6	6	12	67	63	65
>14	6	7	13	83	71	77
All	40	70	110	73	59	64
			Northwest Wind			
0-04	15	19	34	100	63	79
4-09	25	20	45	100	90	96
9-14	25	1	26	96	0	92
>14	--	--	--	--	--	--
All	65	40	105	98	75	90

Hours after sunset: [a] $0.5 \le \text{Early} < 1.75$, [b] $0.75 \le \text{Late} < 4$, [c] $0.5 \le \text{All} < 4$

[d] No winds in this class.

With SW and NW winds, alignment occurred more frequently early in the evening (0.5 - 1.8 hr after sunset) compared with late evening (1.8 - 4.0 hr after sunset). Early and late alignment frequency was similar for NE and SE wind directions. Some alignment occurred for all wind speeds. There was a trend for increasing frequency of alignment with increasing wind speeds.

Consequences of Orientation. Our simulations delineated fallout areas and drift for selected wind speeds, insect airspeeds, source areas, and duration of migration (Fig. 3). If there is zero fallout of oriented migrants during Tmig, then drift distance (Mdist = 180 km, Fig. 3a) is constant for all crab angles, and drift direction equals crab angle. Drift for constant fallout (Figs. 3b and 3d) is not simulated because the mean location of the migrants depends on the rate of fallout versus time. For example, if most of the fallout occurs early during the migration period, then the mean location of the migrants will be near the source area. Random insect

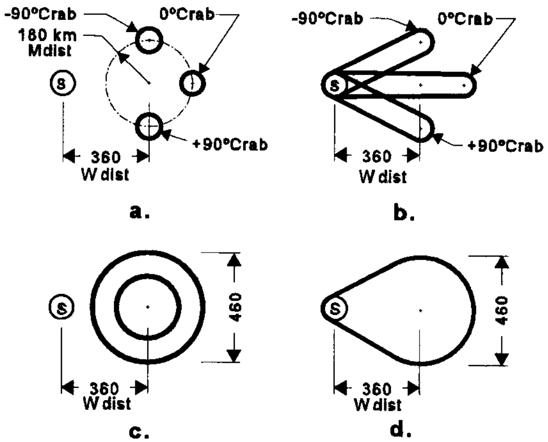

Fig. 3 Simulation of insect migration from a 100 km diameter source area (S) after a 10 hr migration period (Tmig). Destinations and fallout areas are for: (a) uniform orientation and zero fallout during Tmig; (b) uniform orientation and continuous fallout; (c) random orientation and zero fallout during Tmig; and (d) random orientation with continuous fallout. Areas within wide-lines represent fallout areas. Wind is 10 m/s from the west, moth airspeed is 5 m/s, and all variances are equal to zero. Mdist and Wdist are migrant and wind displacement distances during Tmig.

orientation and zero fallout during Tmig produce zero drift (Fig. 3c). Fallout occurs within the annulus of Fig. 3c because of our extreme assumptions and the diameter of the source area is less than the flight distance of individual migrants.

The ratio of migrant to wind displacement distance (Mdist/Wdist) is the error that occurs when wind trajectory models simulate mean displacement of flying migrants. In our simulation of zero fallout during migration, the ratio (error) is 0.5 or 0.0 if migrants are collectively (Fig. 3a) or randomly (Fig. 3c) oriented, respectively. The magnitude and direction of the error depends on mean location of migrants after fallout and wind displacement.

A large fallout area compared with the source area results in a large value of Rfa. Thus any behavior that affects fallout area also affects Rfa. For any source area (S), the smallest fallout area (Rfa = 1) occurs with uniform orientation and zero fallout during Tmig (Fig. 3a). This behavior produces one value of Rfa for all crab angles. Maximum Rfa occurs with random orientation and constant fallout (Fig. 3d). Other combinations of insect behavior produce intermediate values of Rfa (Figs. 3b and 3c).

Source areas of 10 km and 100 km diameter have identical values of Rfa and drift distance when behavior includes collective orientation, any crab angle, and zero fallout during Tmig (Table 5). However, if constant fallout occurs during random orientation, the Rfa values are 1,556 and 24 for source area diameters of 10 and 100 km, respectively.

The concentration of migrants (number per hectare) in a fallout area varies inversely with the fallout area. Thus, any behavior that reduces fallout area also increases migrant concentration in the fallout area.

DISCUSSION

Alignment behavior in this report applies to *H. zea* and *S. frugiperda* moths because these species (a) dominated soil samples, (b) emerged during the periods of radar observations (Pair et al. 1991, Raulston et al. 1995), (c) dominated visual observations using a spot-light and night-vision equipment (Wolf et al. 1994), and (d) have radar cross sections (Wolf, 1993) consistent with the maximum range of targets detected by the radar. A large crab angle in this report represents an insect flight behavior that may affect the destination (left or right of the wind track) of the migrants by hundreds of kilometers in one night.

Frequent crosswind alignment occurred when the wind was from the SE. These insects may be "choosing winds that are close to their preferred compass direction", as proposed by

TABLE 5. Simulated Drift and Rfa (Fallout Area / Source Area) for Different Insect Behaviors.[a]

Insect Behavior				Rfa	
Fallout During Tmig	Crab Angle	Drift Dist.[b] After Tmig	Drift Direct.[c] After Tmig	10 km Diameter Source Area	100 km Diameter Source Area
Zero	180°	180 km	180°	1	1
Zero	-90°	180	-90°	1	1
Zero	0°	180	0°	1	1
Zero	Random	0	0	144	14
Continuous	180°	-- [d]	-- [d]	24	3
Continuous	-90°	--	--	52	6
Continuous	0°	--	--	70	8
Continuous	Random	--	--	1,556	24

[a] Insect Air Speed is 5 m/s, Wind Speed is 10 m/s, and Flight Period is 10 hr (Tmig).

[b] Distance of center of migrants from wind displacement.

[c] Direction of center of migrants from wind displacement.

[d] Mean location of migrants at end of Tmig depends on fallout versus time.

Baker (1978). A NE orientation in a SE wind would displace migrants toward northern Texas and central Oklahoma. During subsequent flights, migrants would be displaced into the central U.S. by prevailing SW nocturnal low-level wind jets (Bonner 1968). By contrast, diametrical orientation toward the SW would displace migrants toward the arid regions of Texas and away from the region of strong low-level wind jets. Unfortunately, preferred migration direction cannot be determined solely from alignment data due to the inherent ±180° ambiguity of the actual orientation. However, during SE and NE winds, the time-lapse film indicated insects were drifting to the left or right of the wind, respectively. If similar behavior occurs during strong winds, then the implied preferred migration direction would be between 135° and 315°.

Another remarkable behavior was the mean alignment between 0° and 90° when winds were from the NE, SE, SW, or NW. This result implies a tendency for orientation within the NE or SW quadrants for all wind directions. Thus, the insects were not cuing exclusively on wind direction. If this behavior occurs during other seasons and at different geographical locations, it may help identify the cues being used for orientation.

Frequency of occurrence of insect alignment was not weighted for low or high insect concentration. Each measurement of alignment was based on the pattern of targets on the radar display, not the quantity of targets. Therefore, these values relate occurrence of the alignment to wind velocity, direction, and time. Also, our alignment measurements reflect behavior near the source area. Flight behavior downwind of source areas is presently unknown. Insect airspeed, flight altitude, duration of flight, fallout as a function of time, and orientation with respect to the winds encountered during migration are necessary parameters for modifying meteorological models to account for insect behavior during migration.

Data for this study were collected during May and June. Behavior during other times of year may be different. For migrating *H. zea* and *S. frugiperda* moths departing a source area, these data suggest that (a) the frequency of occurrence of alignment is influenced by wind speed, (b) crab angles vary with wind quadrant, and (c) alignment is perpendicular to the wind direction when the wind is from the Southeast. The frequent collective orientation, flight above 100 m, multiple generations per season, and long distance of movement (Wolf et al. 1990) appears to meet the criteria of undistracted flight and application of the term "migratory flight" (Johnson 1969) for these insects.

Simulations provided evaluations of some physical consequences resulting from collective orientation during migration. We used extreme assumptions about flight behavior to estimate the minimum and maximum effects. The simulations show that collective orientation increases drift and reduces the size of fallout area. Naturally, a reduction in fallout area increases migrant concentration. Minimum fallout area occurs with collective orientation and no fallout until the end of Tmig. Maximum fallout area occurs with random orientation and constant fallout during Tmig. Real-world variances in wind and insect behavior will affect the size of fallout areas.

Simulations show that fallout during the migration period affects the mean location of the migrants. Therefore, atmospheric trajectories used to estimate migration displacement should be adjusted for active insect flight if some migrants fallout before the end of Tmig or if migrants are oriented. The adjustment should use the mean location of the migrants with respect to the mean wind displacement and atmospheric dispersion. Since Rfa decreases as source area increases, the significance of orientation behavior also decreases as source area increases. Also, significance of orientation behavior decreases as wind speed increases. The impact of migratory behavior on agricultural production or genetic mixing was not simulated.

Maximum fallout area of dispersing insects can be simulated by assuming random orientation, constant fallout, and selecting values for size of source area, wind speed, insect airspeed, and maximum flight duration. Improved estimates of fallout areas require expenditures of research resources to acquire appropriate knowledge about flight behavior and wind vectors at altitudes where the insects fly.

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