Aggregation and Dispersal Behavior of Marked and Released European Corn Borer (Lepidoptera: Crambidae) Adults

William B. Showers  
*Iowa State University*

Richard L. Hellmich  
*Iowa State University*, richard.hellmich@ars.usda.gov

M. Ellison Derrick-Robinson  
*Iowa State University*

William H. Hendrix III  
*Iowa State University*

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Aggregation and Dispersal Behavior of Marked and Released European Corn Borer (Lepidoptera: Crambidae) Adults

Abstract
To observe the aggregation and dispersal behavior of adult European corn borer, Ostrinia nubilalis (Hu¨bner), males in search of mates, two populations were marked, each with a different dye. One population was continuously reared in the laboratory (.5 yr) and the other was collected annually from the Þeld. From 1986 to 1988, marked adults were released in two release sets per year, with three to Þve releases per release set, coinciding with the spring and summer ßights of European corn borer in central Iowa. Traps for recapture contained lures baited with 40 mg of synthetic 97:3 Z:E-11-tetradecenyl acetate. Traplines extended from 200 m to 48 km. Each trap was assigned a compass direction. Males from the laboratory-reared population dispersed similarly to males just 1 generation from the wild. European corn borer males and females dispersed 23Ð49 km and some were recovered 14 km from the release site within 100 min after release. Sampling of aggregation sites demonstrated that on the nights of release, many adults aggregated in adjacent dense vegetation and did not disperse until the following night. Upon dispersal, these adults seemingly moved many meters or kilometers before settling again. Recapture of marked adults at 200 m might have been inßuenced by open landscapes (short, vegetative-growth corn). Recapture at 800 m or beyond, however, was unaffected by open landscapes, and in 1988 a greater proportion of marked males was recaptured while the landscape was closed. (tall, mature-growth corn). In 1987, during the Þrst ßight of European corn borer, displacement to 800 m was southeasterly, south, or west, but during ßrst ßights in 1986 and 1988, displacement to 800m was predominately northeasterly. During the second ßight in midsummer, displacement to 800 m for all 3 yr of the study also was northeasterly. Recapture results from 1986 suggest that male movement.800mis common. During the Þrst release set (early summer), 37% of the males recaptured ßew 800 m or more and 8% ßew 3.2 km or more. During the second release set (late summer), 51% of the males recaptured ßew 800 m or more and 11% ßew 3.2 km or more. The recommendation for placement of nontransgenic corn (Zea mays L.) as refuge in the Corn Belt is a half mile or closer to Bacillus thuringiensis Berliner (Bt)-corn if the refuge corn is not sprayed and a quarter mile or closer when the refuge corn is sprayed. Based on the dispersal results from this study, at least in Iowa, a half-mile proximity recommendation should be robust. Studies still should be conducted in other regions, especially where corn is commonly irrigated, to determine whether European corn borer adult movement patterns are similar.

Keywords
Ostrinia nubilalis, aggregation sites, dispersal, surface airßow, mate seeking, refuge, corn insects and crop genetics research unit, Iowa Agriculture and Home Economics Experiment Station

Disciplines
Agricultural Science | Entomology

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Author(s): William B. Showers, Richard L. Hellmich, M. Ellison Derrick-Robinson, and William H. Hendrix
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WILLIAM B. SHOWERS, RICHARD L. HELLMICH, M. ELLISON DERRICK-ROBINSON, AND WILLIAM H. HENDRIX, III

Corn Insects and Crop Genetics Research Unit, USDA-ARS, and Department of Entomology, Iowa Agriculture and Home Economics Experiment Station, Iowa State University, Ames, IA 50011

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ABSTRACT To observe the aggregation and dispersal behavior of adult European corn borer, Ostrinia nubilalis (Hübner), males in search of mates, two populations were marked, each with a different dye. One population was continuously reared in the laboratory (>5 yr) and the other was collected annually from the field. From 1986 to 1988, marked adults were released in two release sets per year, with three to five releases per release set, coinciding with the spring and summer flights of European corn borer in central Iowa. Traps for recapture contained lures baited with 40 μg of synthetic 97:3 Z:E-11-tetradecenyl acetate. Traplines extended from 200 m to 48 km. Each trap was assigned a compass direction. Males from the laboratory-reared population dispersed similarly to males just 1 generation from the wild. European corn borer males and females dispersed 23—49 km and some were recovered 14 km from the release site within 100 min after release. Sampling of aggregation sites demonstrated that on the nights of release, many adults aggregated in adjacent dense vegetation and did not disperse until the following night. Upon dispersal, these adults seemingly moved many meters or kilometers before settling again. Recapture of marked adults at 200 m might have been influenced by open landscapes (short, vegetative-growth corn). Recapture at 800 m or beyond, however, was unaffected by open landscapes, and in 1988 a greater proportion of marked males was recaptured while the landscape was closed. (tall, mature-growth corn). In 1987, during the first flight of European corn borer, displacement to 800 m was southeasterly, south, or west, but during first flights in 1986 and 1988, displacement to 800 m was predominately northeasterly. During the second flight in midsummer, displacement to 800 m for all 3 yr of the study also was northeasterly. Recapture results from 1986 suggest that male movement >800 m is common. During the first release set (early summer), 37% of the males recaptured flew 800 m or more and 8% flew 3.2 km or more. During the second release set (late summer), 51% of the males recaptured flew 800 m or more and 11% flew 3.2 km or more. The recommendation for placement of nontransgenic corn (Zea mays L.) as refuge in the Corn Belt is a half mile or closer to Bacillus thuringiensis Berliner (Bt)-corn if the refuge corn is not sprayed and a quarter mile or closer when the refuge corn is sprayed. Based on the dispersal results from this study, at least in Iowa, a half-mile proximity recommendation should be robust. Studies still should be conducted in other regions, especially where corn is commonly irrigated, to determine whether European corn borer adult movement patterns are similar.

KEY WORDS Ostrinia nubilalis, aggregation sites, dispersal, surface airflow, mate seeking, refuge
seed companies have focused attention on a high Bt-dose, refuge-management strategy (Hurley et al. 1997). The refuge serves as the source of adult insects that have not been exposed to Bt-corn that then mate with the potentially few resistant adults emerging from high Bt-dose corn. There has been considerable debate on the type, size, and placement of refuge. For European corn borer management, refuge would include any non-Bt host such as corn, potatoes, sweet corn, cotton, peppers, or native weeds that occur near Bt-corn (Ostlie et al. 1997). For this management strategy to be viable, two questions need to be addressed: (1) Is mating random and (2) How far do European corn borer males fly from a non-Bt-source, or from a Bt-source, to find a mate? Answers to these questions could determine refuge size and placement. This study was originally conducted to examine the dispersal behavior of European corn borer males in search of mates. But with the advent of transgenic crops and the question of where to place refuge, this study has taken on a more practical nature involving resistance management.

Materials and Methods

To document the dispersal behavior of mate-seeking European corn borer males, a mark-release-recapture study was conducted in central Iowa during the late spring to late summer, 1986–1988. Males and females were marked internally with one of two dyes (see below) and released for recapture in traps baited with the conspecific sex pheromone (Glover et al. 1987). Although the trapping system was designed for recapture of males, a few females also were recaptured.

Two European corn borer populations, collected in central Iowa, were observed during part of this 3-yr study. As of 1986, one population of European corn borer was descended from a colony that had been maintained for 5 yr in the laboratory (referred to as laboratory). The other population (referred to as Iowa) was descended from field-collected larvae in the autumn of each year and brought out of diapause in the laboratory during late winter. Upon emergence, adults mated and resulting eggs were heat-treated (43°C for 40 min) to reduce field-contracted Nosema pyrausta (Pailloit) infections. To increase numbers, larvae were placed on meridic diet (Guthrie 1987) for 1 generation. Second-generation larvae of the Iowa population and a synchronous generation of the laboratory population were reared on meridic diet containing the lipid-soluble dyes Sudan red no. 470 or Sudan blue no. 670III (BASF, Holland, MI). Dye solutions (6 g of dye dissolved in 60 ml of corn oil) were added to diet for a final dye weight/diet volume ratio of 0.6 g/liter (Ostlie et al. 1984). During 1986 and 1987, to determine whether dye was affecting adult behavior, we reared the laboratory and Iowa populations alternately on the two dyes so that the population reared on Sudan red for the first release set would be reared on Sudan blue for the second release set and so on.

Reed et al. (1972) described rearing procedures. Briefly, just before pupation, larvae move out of the diet and into a waxed, corrugated paper ring fitted into the top of each rearing dish. After ~50–90% of the larvae within each ring pupated, the rings were harvested and hanged in 4–6 emergence cages similar to those described by Showers et al. (1989a). These cages each held ~44 rings and each ring contained from 400 to 600 pupae. Cages were maintained at 15.6°C and a 24-h scotophase to enhance dark adaptation of the emerging adults. On release nights, just before dusk, the cages were transported to an open field surrounded by mixed vegetation. Release began immediately after dusk. At 0500 hours (CST), on the morning after each release, cages were closed and returned to the holding chamber. This procedure was repeated until the release set was completed.

A release set consisted of three to five releases. Percentage of emergence, number of adults capable of flight, and sex ratio were estimated for each release. Two pupal rings were placed within each of two modified (with a floor) Texas 70–50 cm cone traps (Hartstack et al. 1979) stationed at the release site. Adults captured in the receptacle placed above the cone were classified as capable of flight only if there were no abnormalities similar to the abnormalities for Agrotis ipsilon (Hufnagel) described by Showers et al. (1989a). Capture data were extrapolated to the numbers of adults emerging from the adjacent release cages.

To determine whether the released adults were staying near the release site, flush bar samples (Sappington and Showers 1983b) of 10 m² were taken in adjacent vegetation: giant, green, and yellow foxtail grasses, Setaria spp.; bromegrass, Bromus spp.; smartweed, Polygonum pensylvanicum L.; and alfalfa, Medicago sativa L. Sampling consisted of sweeping an aluminum bar (1 m long) through the plant canopies in 10 consecutive meter-sweeps. The numbers of European corn borer adults flushed were counted and totaled per sample site each day. Wild and released adults were indistinguishable, so these counts contained both. Flush bar counts were taken before 0830 hours (CST) while temperatures were cool and surface airflow was <10 km/h. Sampling began the morning after each release and continued consecutively for 2–4 d.

Pheromone trapping was conducted annually during late spring to late summer, 1986–1988, on the Iowa State University Research Farm, Ankeny, IA, and surrounding areas within central Iowa. The Research Farm is typical of central Iowa; it consists of 600 ha of corn and soybeans, Glycine max (L.) Merrill, with 3 riparian zones running through it. Central Iowa is platted with section roads running from north to south and east to west. Therefore, traps were stationed on these section roads so that the traplines were arranged in squares. Fig. 1 illustrates 3 of 5 traplines in central Iowa that surrounded a release site on the Research Farm during 1988, 0.5 km (800 m), 5.6 km, and 38.4 km. The trapline distance is accurate only on the cardinal points of the compass. Therefore, traps sta-
Recapture data were collected in wing-type traps (26 by 20 by 11 cm) (Pherocon IC; Trécé, Salinas, CA, or Scentry, Buckeye, AZ) with adhesive reinforced with Tack-Trap (Animal Repellents, Griffin, GA) uniformly coated on the interior bottom panel. Each trap was baited with 40 μg of synthetic 97:3 ZE-11-tetradecenyl acetate (Trécé), the conspecific female sex pheromone (Glover et al. 1987). Pheromone was impregnated in a rubber septum (Trécé). Traps were placed 2 m above the soil surface. During 1986, there were 6 traplines: 200 m (16 traps, 100 m apart), 500 m (32 traps, 200 m apart), 3.2 km (64 traps, 200 m apart), 16 km (40 traps, 3.2 km apart), 32 km (44 traps, 6.4 km apart), and 64 km (55 traps, 9.6 km apart). In 1987, traplines were placed at 500 m (32 traps, 200 m apart), 9.6 km (47 traps, 1.6 km apart), 19.2 km (91 traps, 1.6 km apart), and 38.4 km (162 traps, 1.6 km apart). During 1988, there were 5 traplines placed at 500 m (32 traps, 200 m apart), 25.6 km (66 traps, 3.2 km apart), 32 km (82 traps, 3.2 km apart), 38.4 km (98 traps, 3.2 km apart), and 48 km (128 traps, 3.2 km apart). During the second and third years of the study, to enhance recapture of marked males on the more distant traplines, traps were stationed an equal distance within each line (1987, 1.6 km, 1988, 3.2 km).

Each trap on each square was assigned a degree of the compass to denote direction. Traps assigned compass degrees 0–23 or 337–360 represented north, traps assigned compass degrees 24–68 represented northeast, traps assigned compass degrees 69–113 represented east, and so on. Speed and direction of nightly surface airflow were recorded with a Mark III anemometer (Climatronics, Bohemia, NY) stationed at the release site. Malfunctions produced some gaps in the nightly data.

Traps were observed the day after the night of release and for 1–3 d thereafter (total of 2–4 d). All traps received fresh sex pheromone and new bottom panels after 4 nights. The bodies of all captured adults on all traplines were pulled apart exposing the fat bodies. The marked fat bodies of adults recaptured on the 200-m or 800-m traplines were recorded at the trap site. If there was some question, then the adult was treated similar to those adults presumed to be dye-marked beginning with the 3.2-km trapline. These adults were placed in plastic diet cups with trap number, trapline, and date marked on the cup and returned to the laboratory for fat body color analysis according to Showers et al. (1993).

During 1986, there were two release sets: 5 July–16 July and 25 July–9 August. There were five releases for both release sets. The first release set corresponded with corn growth of 9–13 leaves or vegetative stages V9 to V13 (Ritchie et al. 1989), and with corn growth the landscape began to close. This corn growth stage usually corresponds with the beginning of the summer (second) flight of European corn borer in central Iowa (Showers et al. 1989b). Corn growth during the second release set ranged from 17 leaves to the reproductive stage called kernel blister, V17 to R2. During this stage, the landscape is closed because nearly all cornfields in central Iowa are mature. The summer flight is usually very heavy during this time.

During 1987, there were also two release sets: 11 June–24 June and 8 July–23 July. The first release set consisted of five releases; the second release set consisted of three releases. The first release set occurred while corn growth ranged from five to eight leaves, V5 to V8. The landscape was open or unimpeded. The spring (first) flight is usually synchronous with this growth period. The second release set was conducted while corn plants had 9–17 leaves, V9 to V17; thus, the landscape had begun to close. The summer flight usually occurs during these corn growth stages.

Two release sets were conducted during the summer of 1988: 13 June–30 June and 11 July–29 July. The first set consisted of five releases and the second set consisted of four releases. Only the Iowa population was released. During the first release set, corn plants grew from six to nine leaves, V6 to V9, and the landscape was open and unimpeded. The second release set occurred while corn growth was 10 leaves to the reproductive stage of silking, V10 to R1. These mature cornfields closed the landscape. Similar to 1987, these times coincided with the first and second flights, respectively, of European corn borer adults in central Iowa.

The mark-release-recapture studies were one-release site descriptive studies over vast landscape and days. This was a descriptive study designed to determine a general pattern of European corn borer movement for this area. The area covered was so large that multiple release sites necessary for an experimental study could not be entertained. This study was designed as a randomized complete block with a factorial arrangement. Each release set was a separate study. Release times within release sets were treated as ran-
dom replicates; variables were trap distance from release, days after release, compass degrees from release, and population type.

To standardize the recapture data for distance from the release site, they were transformed to proportion males recaptured per trap per 10,000 marked males released. Proportions recaptured per distance per night of the total recaptured also were calculated. Data collected for the directional part of the studies were averaged over traps that represented a specified compass direction. All tests were subjected to analyses of variance (ANOVA) with SAS (PROC GLM, SAS Institute 1985) and means were separated with the Waller—Duncan K-ratio t-test (Waller and Duncan 1969). Analyses were approximate with the focus on pattern in proportion or mean number recaptured rather than variances.

Studies to estimate the number of European corn borer adults in vegetation adjacent to the release site also were designed as a randomized complete block. Times of adult release were random replicates with days after release and vegetation type as variables. In some of these flush bar studies, distance of the vegetation from the release site was also a variable. Daily flush bar counts were averaged over releases for days within release sets, and ANOVAs were conducted. Mean separations were conducted with the Waller—Duncan K-ratio t-test.

Results

Laboratory and Iowa Populations, 1986 and 1987.

Dye type was nonsignificant for recapture of European corn borer males within and between release sets within years and between years. Proportions (±SE) of laboratory and Iowa males recaptured per trap per 10,000 released also were nonsignificant during 1986 [0.391 ± 0.093 versus 0.278 ± 0.132 for release set 1 (F = 0.50, df = 1, 44; P = 0.483), and 0.164 ± 0.038 versus 0.189 ± 0.057 for release set 2 (F = 0.13; df = 1, 56; P = 0.724)] and 1987 [0.411 ± 0.164 versus 0.309 ± 0.095 for release set 1 (F = 0.28; df = 1, 30; P = 0.601), and 0.053 ± 0.028 versus 0.063 ± 0.028 for release set 2 (F = 0.07; df = 1, 20; P = 0.798)]. Therefore, we combined the recapture data for the two populations for each release set for the 2 yr of the study that both populations were released.

Dispersal of Marked European Corn Borer Males.

For the first release set of 1986, an estimated 161,389 marked males and 122,047 marked females, capable of normal flight, were released over five releases. A total of 496 marked males (0.31% of total) was recaptured on the 200-m, 800-m, and 3.2-km traplines. Just 170 wild European corn borer males were captured on these three traplines. There were no recaptures of marked males on the 16-, 32-, or 64-km traplines. Night effect was not significant (F = 0.27; df = 2, 20; P = 0.763), but distance was a significant factor (F = 4.52; df = 2, 20; P = 0.020). The highest proportion of males (±SE) was recaptured at 200 m (0.382 ± 0.105), followed by 800 m (0.083 ± 0.026), and the fewest at 3,200 m (0.011 ± 0.005) (Table 1, 1986, release set 1).

For the second release set of 1986, an estimated 128,986 marked males and 96,271 marked females, capable of normal flight, were released over five releases with a total of 265 marked males (0.28% of total) recaptured on all traplines. There were 3,330 wild European corn borer males captured on just the 200-m, 800-m, and 3.2-km traplines. The night-by-distance interaction was nearly significant (F = 2.29; df = 4, 26; P = 0.086), and the night and distance factors were significant [(night: F = 4.03; df = 2, 26; P = 0.030); (distance: F = 7.74; df = 2, 26; P = 0.002). Distance that males were recaptured from the release site suggested a trend for more males being recaptured at 200 m, the next largest number at 800 m, and the fewest at 3.2 km. The highest proportion of males was recaptured the second night, but by the third night, proportions of males caught at 200 and 800 m were similar (Table 1, 1986, release set 2). One Iowa male was collected three August 1986 on the 9.6-km trapline. The calculated hypotenuse indicated that this moth had dispersed ~11.52 km southwest of the release site (Fig. 2). One laboratory male was collected 7 August on the 6.4-km trapline. This trap was located 6.84 km north of the release site (Fig. 2). Marked males were not recaptured on the 16-km trapline.

To determine whether recapture was greater in V9 to V13 corn (landscape partly open) compared with V17 to R2 (landscape closed), an analysis was conducted with release set as a factor. Recapture of European corn borer males during the time when corn was shorter was significant (F = 4.21; df = 1, 50; P = 0.046). The proportional recapture per trap was 0.159 ± 0.045 during V9 to V13 and 0.079 ± 0.020 during V17 to R2. But when proportions of males recaptured on the 200-m trapline were dropped from the analysis, release set was not significant (release set 1: 0.047 ± 0.015, release set 2: 0.037 ± 0.008; F = 0.93; df = 1, 31; P = 0.344).

For the first release set of 1987, an estimated 98,936 marked males and 91,326 marked females, capable of normal flight, were released over five releases with a total of 319 marked males recaptured (0.32% of total released). There were 143 wild European corn borer males captured on the 800-m and 9.6-km traplines. The numbers recaptured between nights were similar (F = 0.46; df = 1, 13; P = 0.644). Distance that males were recaptured from the release site was significant (F = 9.41; df = 1, 13; P = 0.009), more males were recaptured per trap at 800 m (0.474 ± 0.162) than at 9.6 km (0.043 ± 0.022) (Table 1, 1987, release set 1). Furthermore, two Iowa males were collected on the 19.2-km trapline. One was collected on 20 June, located 20.10 km northwest of the release site. The second male was collected on 23 June, located 22.92 km to the northwest of the release site (Fig. 2). Marked adults were not recaptured on the 38.4-km trapline.

For the second release set, an estimated 77,706 marked males and 71,730 marked females, capable of
normal flight, were released over three releases with a total of 112 marked males recaptured (0.14% of total released) on the 800-m trapline. The numbers recaptured between nights were similar ($F = 0.10; df = 2, 10; P = 0.909$) (Table 1; 1986, release set 2). Marked males were not recaptured on the 9.6-, 19.2-, or the 38.4-km traplines. Wild European corn borer males were captured on all traplines, but there were just 92 on the 800-m (69 males) and 9.6-km (23 males) traplines.

An analysis was conducted with release set as a factor to determine whether more males were captured in an open landscape (V5 to V8) or closed landscape (V9 to V17) on the 800-m trapline. Proportion of males recaptured during the two release sets were not significantly different ($F = 0.01; df = 1, 25; P = 0.912$).

During the first release set of 1988, an estimated 99,828 marked Iowa males and 92,149 marked Iowa females, capable of normal flight, were released over four releases. A total of 118 marked males (0.12% of total released) and two marked females was recaptured. There were 116 marked males recaptured and 183 wild males captured on the 800-m trapline. The proportions of marked males recaptured between nights on the 800-m trapline were not significantly different ($F = 1.92; df = 4, 7; P = 0.212$). But the trend was for most adults to be out of the area of the release site by the third night (Table 1; 1988, release set 1). On the night of one release (13 June), we randomly sampled European corn borer adults in flight. At 2300 hours a swarm of 10 or 11 European corn borer adults crossed the path of a vehicle and three hit the windshield. The fat bodies (Showers et al. 1993) of the three were colored red—two unmated females and one male. The calculated hypotenuse indicated the adults had traveled 14.2-km north-northeast within 100 min after release (Fig. 2). Airflow was south-southeast to south at 1.6–3.2 km/h. Therefore, these adults would have had to travel 2.36 m/s or 8.46 km/h to arrive at the distance of recapture by 2300 hours. On 18 June, a marked male was collected on the 25.6-km trapline. This trap was 26.5 km north-northeast of the release site (Fig. 2). During this time marked adults

### Table 1. Recapture of marked European corn borer males in sex pheromone traps at specific distances from a release site in central Iowa.

<table>
<thead>
<tr>
<th>Year</th>
<th>Set</th>
<th>Night</th>
<th>Proportion (per 10,000 released) captured per trap</th>
<th>% total captured</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>n</td>
<td>200 m</td>
<td>n 800 m</td>
</tr>
<tr>
<td>1986</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>0.33 (0.27)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>5</td>
<td>0.50 (0.43)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>1</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>5</td>
<td>0.09 (0.06)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>4</td>
<td>0.07 (0.04)</td>
</tr>
<tr>
<td>1987</td>
<td>1</td>
<td>1</td>
<td>5</td>
<td>0.38 (0.55)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>5</td>
<td>0.60 (0.73)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>3</td>
<td>0.41 (0.55)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>3</td>
<td>0.08 (0.11)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>3</td>
<td>0.10 (0.10)</td>
</tr>
<tr>
<td>1988</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>0.08 (0.07)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>4</td>
<td>0.23 (0.19)</td>
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<tr>
<td></td>
<td></td>
<td>3</td>
<td>3</td>
<td>0.23 (0.23)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>2</td>
<td>0.06 (0.06)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>2</td>
<td>0.03 (0.04)</td>
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<td></td>
<td>2</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>5</td>
<td>0.53 (0.37)</td>
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<td></td>
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<td>3</td>
<td>5</td>
<td>0.53 (0.52)</td>
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<tr>
<td></td>
<td></td>
<td>4</td>
<td>2</td>
<td>0.62 (0.36)</td>
</tr>
</tbody>
</table>

Presented as proportion (per 10,000 released) captured per trap at each distance and night averaged over all reps in a release set, and proportion of total captured at each distance and day averaged over all reps in a release set. Number in parentheses following each mean is standard deviation.
were not recaptured on the 32-, 38.4-, or 48-km traplines.

During the second release set of 1988, an estimated 80,726 marked males and 74,516 marked females, capable of normal flight, were released over five releases with a total of 270 marked males (0.33% of total released) and 1 marked female recaptured. There were 268 marked males recaptured and 582 wild males captured on the 500-m trapline. The proportion of marked males recaptured over four nights on the 500-m trapline was not significantly different ($F = 1.65; df = 4, 9; P = 0.245$). Although the highest proportion seemingly was recaptured the first night, the standard deviation mediated any difference (Table 1; 1988, release set 2). Three adults, two males and one female, all captured on the 38.4-km trapline, were marked. One male was collected on 25 July, 40.3 km almost due west of the release site (Fig. 2). On 29 July, a male was collected 40.2 km north-northeast of the release site, and a female was collected 49.1 km northwest of the release site (Fig. 2). This female had mated (class 3, Showers et al. 1974) before recapture.

To determine whether recapture of marked males on the 500-m trapline was greater with an open landscape (V6 to V9) than after the landscape began to close (V10 to R1), an analysis was conducted with release set as a factor. Significantly ($F = 8.01; df = 1, 19; P = 0.011$) greater recapture of marked males occurred after the landscape had begun to close (V10 to R1).

Aggregation of European Corn Borer Adults. For release set 1 of 1986 (5 July–16 July), samples were taken in five habitats adjacent to the release site for three mornings after each of the five releases. The standard error ($\pm 2.2$) indicated that the mean number of adults in habitat 3 (giant foxtail and a creek) was significantly different from the mean numbers of adults in habitats 1, 4, and 5 (Fig. 3; 1986, release set 1). Mornings after release were also significant ($F = 29.27; df = 1, 26; P = 0.0001$) with the greatest number of adults being present the first morning after release (Table 2; 1986, release set 1).

Flush bar samples were taken in nine habitats, 25 July–9 August, during release set 2. Samples were taken for three mornings after each of the five releases. Habitat ($F = 3.32; df = 5, 77; P = 0.0026$) was significant. Three of the four most attractive habitats contained giant foxtail (Fig. 3; 1986, release set 2). But if the giant foxtail was mowed (habitat 9) it was no more attractive than yellow foxtail (habitat 7) or bromegrass that had become flat (habitats 1, 6, and 8). Although flowing water (creek) was present in three of the habitats, its influence was negligible. Mornings after release were significant ($F = 11.66; df = 2, 77; P = 0.0001$). Although many adults might have left the area the night of release, some went to nearby aggregation sites, spent the night, and left the night after release (Table 2; 1986, release set 2). Few remained in the area, however, the second or third mornings after release.

Samples were taken in various vegetative habitats, 12 June–20 June 1987. Variation between replicates during the first release set was considerable and approached significance ($F = 2.41; df = 3, 57; P = 0.0715$). There were 10 habitats and bromegrass was present to some degree in all of them; foxtail was just beginning to develop in some of the locations. Habitat 1, dense bromegrass and alfalfa, averaged 81.6 ± 10.0 adults, a far greater number than in the other habitats (Fig. 3; 1987, release set 1). Habitat 6, dense bromegrass at the edge of a creek, averaged 40.0 ± 10.0 adults, a considerably greater number than the average in habitats 2 and 10, both with sparse bromegrass (Fig. 3; 1987, release set 1). Mornings after release were significant ($F = 12.96; df = 1, 57; P = 0.0007$). As in 1986, many adults might have left the area the night...
of release, but others went to nearby aggregation sites and spent the night, but left the night after release (Table 2; 1987, release set 1).

Flush bar samples were taken 9–20 July during release set 2 in the same 10 habitats that had been sampled during release set 1. The greatest differences in the habitats between the two release sets were the development of giant foxtail and the structural decline in bromegrass. The mean numbers of European corn borer adults at a distance of 144 m from the release site. Mornings after release were significant (Table 2; 1987, release set 2). Although dense bromegrass (habitat 2) was still attractive, it was less so than a bromegrass-giant foxtail mix. But if desirable habitats, such as giant foxtail mix, were in excess of 100 m from the release site, few adults settled in them. Mornings after release were significant (Table 2; 1987, release set 2).

Means followed by the same lowercase letter within years and release sets are not significantly different (P = 0.05, Waller-Duncan K-ratio t-test).

Table 2. Mean (± SE) number of European corn borer adults per 10 m² of various plant habitats near the release site 1, 2, or 3 mornings after release, Ankeny, IA

<table>
<thead>
<tr>
<th>Year</th>
<th>Morning after release</th>
<th>Release Set 1</th>
<th>Release Set 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>1986</td>
<td>1</td>
<td>14.6 ± 1.7a</td>
<td>17.8 ± 1.8a</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>9.0 ± 1.3b</td>
<td>6.8 ± 2.3b</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>3.0 ± 2.9c</td>
<td>6.3 ± 2.1b</td>
</tr>
<tr>
<td>1987</td>
<td>1</td>
<td>26.4 ± 4.5a</td>
<td>10.2 ± 0.5a</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>3.8 ± 1.5b</td>
<td>1.1 ± 0.9b</td>
</tr>
<tr>
<td>1988</td>
<td>1</td>
<td>9.4 ± 1.8a</td>
<td>7.6 ± 1.5a</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>4.2 ± 1.8b</td>
<td>0.4 ± 1.5b</td>
</tr>
</tbody>
</table>

Means followed by the same lowercase letter within years and release sets are not significantly different (P = 0.05, Waller-Duncan K-ratio t-test).

The greatest mean numbers occurring in habitats consisting of a mix of bromegrass and giant foxtail 65–70 cm in height and just 5–20 m from the release site (Fig. 4, release set 2). Although dense bromegrass (habitat 2) was still attractive, it was less so than a bromegrass-giant foxtail mix. But if desirable habitats, such as giant foxtail mix, were in excess of 100 m from the release site, few adults settled in them. Mornings after release were significant (Table 2; 1987, release set 2).

Direction of Dispersal of Marked Males. During release set 1 of 1986 (5 July–16 July) at 200 m, there were significant recaptures of males to the east, southeast, southwest, and west. As males dispersed to 800 m, however, significant recaptures were occurring northeast, with trends toward the north and east (Table 3, release set 1). Nightly surface airflow direction and speed were variable but usually southerly (135–225°) at 4.8–11.2 km/h.

Release set 2 occurred while the surrounding cornfields were in reproductive stages (V17 to R2). Significantly greater numbers of marked males were recaptured at 200 m south rather than northeast or northwest of the release site. But dispersal of males to 800 m was significantly greater toward the northeast (Table 3, release set 2). Although nightly surface airflow direction and speed were variable, many nights’ airflow was southerly to southwesterly (180–225°) at 7.0–14.4 km/h.

The landscape was open (corn growth stages V5 to V8) during the first release (11 June–24 June) of 1987 and the greatest mean numbers of marked males were recaptured in the south with trends toward the southeast and west of the 800-m tranline (Table 4; 1987, release set 1). On the 9.6-km tranline, the 21 recaptured males were collected as follows: north; north-
east; 0; east; 1; southeast; 1; south; 4; southwest; 1; west; 10; and northwest, 3. During this period (11 June–24 June), nightly surface airflow was predominately east, northeast to north (90, 45–0 [360°]) at 4.0–8.0 km/h. There were, however, two stormy nights, 17 and 18 June and 18 and 19 June, with southerly to southwesternly airflow (180–225°) at 11.2–14.4 km/h. With these magnitudes of airflow, potential displacement of European corn borer adults could have been northerly. Corn growth stages (V9 to V17) and times (5 July–23 July) during release set 2 were somewhat synchronous with corn growth stages (V9 to V13) and times (5 July–16 July) during release set 1 in 1986. Nightly surface airflow patterns were variable but usually southerly to southwesterly (180–225°), with speeds of 3.2–8.0 km/h and gusts to 19.2–24.0 km/h. A significantly greater mean number of marked males was recaptured in the northeast rather than south and west portions of the 800-m tralpine (Table 4; 1988, release set 2). Recapture numbers in the east and southeast were similar to the number recaptured in the northeast. For 7 nights during this period, surface airflow was southeast to west (135, 180, 225–270°) at 1.6–9.6 km/h. On the night of 13 June, when marked adults were recaptured 100 min after release, the south-southwest airflow at 1.6–3.2 km/h was probably instrumental but insufficient to allow the observed adults being 14.18 km north northeast of the release site. There was no northerly surface airflow from 13 to 30 June.

Corn growth stages (V10 to R1) and times (11 July–29 July) during release set 2 were slightly later than for release set 2 of 1987. But similar to the previous year, dispersal toward the northeast portion of the 800-m tralpine was significantly (F = 3.21; df = 7, 21; P = 0.0178) greater. Fewer recaptures of marked European corn borer males occurred in the western portions of the tralpine (Table 4; 1988, release set 2). Nightly surface airflow patterns were variable. There were five nights with southerly to southwesterly (180–225°) airflow at 1.6–6.4 km/h. There were five nights with northeasterly to northerly (45–360°) airflow at 4.8–6.4 km/h. For three nights previous to the collection (25 July) of the marked male 40.3 km west of the release site, there was calm- to-light (1.6 km/h) northeasterly (45°) airflow. Unfortunately, the anemometer had been shut down 2 nights before the collections on 29 July of the male. 40.2 km north -northeast, and the female, 49.1 km northwest, of the release site, respectively.

Direction of Dispersal of Marked European Corn Borer Males at 800 m, 1986–1988. The 800-m tralpine was maintained throughout these studies. An analysis was conducted to determine whether direction of dispersal was significant at 800 m within and between years. Dispersal was observed 11 June–16 July, approximating the time of the first flight and the beginning of the second flight of European corn borer adults in central Iowa, and 11 July–9 August, approximating the beginning through the middle of the second flight. Over years, direction of dispersal was significant (F = 9.77; df = 7, 30; P = 0.0001), but there was a significant interaction between time periods and direction of dispersal (F = 3.07; df = 7, 30; P = 0.0147). Dispersal to the south and west was significantly greater 11 June–16 July, but dispersal to the north and northeast was significantly greater 11 July–9 August (Fig. 5).

Discussion

This study illustrates that some European corn borer males and females disperse distances of 23–49 km in just a few nights and that some disperse 14 km in just a few minutes. There is no direct way from this study to assess whether such movement is rare or common. But there is circumstantial evidence from

<table>
<thead>
<tr>
<th>Compass degrees</th>
<th>Release set 1</th>
<th>Release set 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 or 360, north</td>
<td>1.9 ± 2.1b</td>
<td>5.0 ± 2.0a</td>
</tr>
<tr>
<td>45, northeast</td>
<td>2.0 ± 2.1b</td>
<td>5.0 ± 2.0a</td>
</tr>
<tr>
<td>90, east</td>
<td>1.9 ± 2.1b</td>
<td>5.0 ± 2.0a</td>
</tr>
<tr>
<td>135, southeast</td>
<td>1.9 ± 2.1b</td>
<td>5.0 ± 2.0a</td>
</tr>
<tr>
<td>180, south</td>
<td>2.0 ± 2.1b</td>
<td>5.0 ± 2.0a</td>
</tr>
<tr>
<td>225, southwest</td>
<td>3.0 ± 2.1b</td>
<td>5.0 ± 2.0a</td>
</tr>
<tr>
<td>270, west</td>
<td>1.9 ± 2.1b</td>
<td>5.0 ± 2.0a</td>
</tr>
<tr>
<td>315, northwest</td>
<td>2.0 ± 2.1b</td>
<td>5.0 ± 2.0a</td>
</tr>
</tbody>
</table>

Means followed by the same lowercase letter within years and distances are not significantly different (P = 0.05, Waller-Duncan K-ratio t-test).

<table>
<thead>
<tr>
<th>Compass degrees</th>
<th>1987 release set</th>
<th>1988 release set</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 or 360, north</td>
<td>8.2 ± 4.0bc</td>
<td>11.5 ± 5.5abc</td>
</tr>
<tr>
<td>45, northeast</td>
<td>6.2 ± 4.0c</td>
<td>19.0 ± 5.5a</td>
</tr>
<tr>
<td>90, east</td>
<td>4.6 ± 4.0c</td>
<td>13.5 ± 5.5ab</td>
</tr>
<tr>
<td>135, southeast</td>
<td>15.4 ± 4.4b</td>
<td>8.5 ± 5.5abc</td>
</tr>
<tr>
<td>180, south</td>
<td>19.0 ± 4.0a</td>
<td>0.0 ± 5.5c</td>
</tr>
<tr>
<td>225, southwest</td>
<td>3.0 ± 4.0c</td>
<td>2.0 ± 5.5c</td>
</tr>
<tr>
<td>270, west</td>
<td>16.0 ± 4.0ab</td>
<td>3.5 ± 5.5bc</td>
</tr>
<tr>
<td>315, northwest</td>
<td>2.0 ± 4.0c</td>
<td>1.0 ± 5.5c</td>
</tr>
</tbody>
</table>

Means followed by the same lowercase letter within years and release sets are not significantly different (P = 0.05, Waller-Duncan K-ratio t-test).
surveys of aggregation sites that the majority of adults dispersed within one or two nights after release. Recapture results from 1986 suggest that male movement >800 m is common. During the first release set, 37% of the males recaptured flew 800 m or more and 8% flew 3.2 km or more. During the second release set, 51% of the males recaptured flew 800 m or more and 11% flew 3.2 km or more. These calculations are based on the proportions of total males recaptured presented in Table 1. These estimates might be low because trap density at 200 m was higher than trap densities at 800 m and 3.2 km.

The recommendation for placements of refuges for Bt-corn in the Corn Belt is a half-mile or closer when refuge corn is not sprayed and a quarter mile or closer when the corn is sprayed (Anderson and Hellmich 2000). Based on the dispersal data from this study, at least in Iowa, a half-mile proximity recommendation should be robust. Rare resistant moths should encounter an ample supply of susceptible moths whether they mate in an aggregation site near field of origin or move to a more distant aggregation site to mate. This assumes that growers in the area plant the recommended amount of nontransgenic corn, currently 20% or more (Anderson and Hellmich 2000). Studies still should be conducted in other regions, especially where corn is commonly irrigated, to determine whether European corn borer adult movement patterns are similar.

Are most European corn borer adults dispersing 25—49 km, or are there only a few founders searching for new habitats to colonize? Perhaps they are founders that have dispersed to these and possibly greater distances. Caffrey and Worthley (1927) hypothesized that European corn borer adults were capable of flying 44 km across Lake Eire. Trapping results from our study suggest that such distances can be obtained perhaps within one night and certainly within a few nights.

Recapture of marked males at 800 m might have been influenced by an open landscape, as it is during the spring flight of European corn borer. At this time the corn canopy would be <2 m in height, therefore flight at or just above the canopy might possibly allow the released males greater access to wind-borne sex pheromone stationed 2 m above ground level. But recapture of marked adults at 800 m or greater distances was unaffected by an open landscape. This result, plus that in 1988 a greater proportion of males was recaptured at 800 m while the landscape was closed, might suggest that recapture at these greater distances resulted from the released males flying some meters above the corn canopy (DeRozari et al. 1977) and the sex pheromone plume. Therefore, they would not have perceived the wind-borne pheromone until after settling out.

One could argue that the high density of adults released influenced European corn borer adult movement. We cannot prove there was no influence, but the numbers of adults in the aggregation areas were not abnormally high. They were consistent with the numbers of adults sampled in aggregation sites during previous studies (Showers et al. 1976, 1980, DeRozari et al. 1977, Sappington and Showers 1983a, 1983b and Derrick and Showers 1990).

Sampling of adult European corn borer within aggregation sites demonstrated that although bromegrass is an important aggregation site for European corn borer adults during spring and early summer (Hellmich et al. 1998), senescing bromegrass with its declining structure during midsummer is relatively unattractive. The proper structure (Pleasants and Bitzer 1999) and microclimate—cool temperatures and very high humidity (DeRozari et al. 1977) needed for mating—usually were not present. During midsummer in Iowa, these necessary attributes are furnished by giant foxtail (Showers et al. 1976) and to a lesser extent green foxtail and soybeans. Surprisingly, during midsummer after the landscape had closed, if desirable habitats for adult aggregation, such as giant foxtail (60—75 cm in height), were >100 m (Showers et al. 1980) from the release site, few adults settled in them. This might indicate a landscape effect (Fig. 4, habitat 9) and that when adults settle in an aggregation site and then disperse, they may move a considerable distance before resettling. This high dispersal of adults and mixing of field populations would suggest that it should not matter whether aggregation sites are near transgenic or refuge cornfields. Large number of adults that have not been exposed to Bt-corn should be present in most aggregation sites.

Distance and direction of European corn borer dispersal seemingly are assisted by surface airflow. Showers et al. (1995) presented evidence that a bivoltine population of European corn borer in North Dakota dispersed mostly north and west on light (<5 km/h) southerly and easterly surface airflow. Chiang et al. (1965) suggested that during the 1960s, substantial numbers of a bivoltine population of European corn borer entered Minnesota from Iowa on southerly surface airflow. In 1987, in central Iowa during late spring and early summer, the period of first flight of European corn borer, displacement to 800 m was usually southeasterly, south, or west. But during this period in 1986 and 1988, displacement to 800 m was predominately northeasterly. In midsummer, the period of second flight of European corn borer, displacement to 800 m and beyond (Fig. 2) for the 3 yr of the study also was predominately northeasterly. Was surface airflow
responsible for these displacements? Probably to a large degree, but those adults recovered 14 km from the release site (13 June 1988) might be indicative of flight of the majority of adults. Interestingly, these adults were flying at least 5.26 km/h faster than displacement by surface airflow (1.6–3.2 km/h).

Another surprising determination was that European corn borer males of a population reared in the laboratory for 5–6 yr dispersed in search of mates similarly to males just one generation removed from the wild. This information may be useful in future studies of European corn borer dispersal. Acquiring large numbers of feral insects annually to start colonies for dispersal research is time-consuming and expensive.

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