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Evidence for obligate migratory flight behavior in young European corn borer (Lepidoptera: Crambidae) females

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Abstract

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Evidence for Obligate Migratory Flight Behavior in Young European Corn Borer (Lepidoptera: Crambidae) Females

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ABSTRACT European corn borer, *Ostrinia nubilalis*, flight behavior was examined in laboratory experiments. Adults were each tethered to 1 of 16 round-about flight mills in an environmental chamber, and the data were relayed to a computer. Parameters analyzed included duration, distance, and speed of the longest continuous flight and total flight time during an 8-h night. Comparisons were made between unmated and mated adults of both sexes at different ages up to 5 d after emergence. For unmated females, duration of the longest flight was highest the first night after emergence, declining significantly by 5 d of age. In contrast, duration of the longest flight for males was lowest at 1 d of age, increasing significantly by 3 d of age. Flight speed of females was roughly twice that of males at all ages. Mating did not affect flight behavior of either sex at any age tested, but mated adults could not be tested before 2 d of age because the first night was needed for mating. The pattern of age-specific flight behavior suggests that unmated females engage in obligate migratory flight the first full night after emergence. The median duration of this flight was ≈2 h in our experiments, with some adults flying continuously for the full 8 h of darkness. Females of other ages and males of all ages tested were capable of long-duration flights, but they more likely represent foraging flight. These results help explain the high dispersal rate of newly emerged adults from release sites in field experiments.

KEY WORDS *Ostrinia nubilalis*, migration, dispersal, flight behavior, flight mill

Understanding the temporal and spatial relationship between European corn borer, *Ostrinia nubilalis* (Hübner), mating and dispersal behavior is of great importance to those designing and implementing insect resistance management (IRM) strategies in relation to transgenic *Bt* corn (Gould 1998, Rice and Pilcher 1998, Showers et al. 2001, Dalecky et al. 2006b, Bailey et al. 2007). Several studies of European corn borer dispersal have been conducted in the field using mark-release-recapture strategies (Hunt et al. 2001, Showers et al. 2001, Qureshi et al. 2005, Dalecky et al. 2006b, Reardon et al. 2006, Bailey et al. 2007, Reardon and Sappington 2007). Previous studies examined temporal rhythms of adult movement into and out of grassy aggregation sites or into traps over the course of a night and related that movement to nightly periodicity in drinking, mating, and oviposition behavior, all of which can be affected by local weather conditions (Loughner 1972, Showers et al. 1974a, 1976, DeRozari et al. 1977, Sappington and Showers 1983a, b). Thus, there is considerable information on local

movement dynamics and behavior adult European corn borers, yet results of these studies often seem contradictory or difficult to reconcile when trying to synthesize them into a coherent picture of adult population dynamics.

Even less is known about the geographic extent to which European corn borer adults disperse from their natal fields. It is often assumed when parameterizing models of *Bt* resistance evolution that the distance an adult moves from its natal field is limited, and such models have served as the basis for requiring the planting of 20% non-*Bt* refuge within 800 m of *Bt* corn (EPA 1998, 2001). In other words, at the time of formulation of the IRM strategy to be implemented with the commercialization of *Bt* corn targeting European corn borer in the United States, most entomologists advising the U.S. Environmental Protection Agency felt comfortable that adult movement was extensive enough to ensure random mixing and mating of the population at only 800-m distance. There is evidence, however, that long-distance movement may be a normal part of the life history of this insect. Range expansion of the species or a trait into virgin territory (Chiang 1972, Showers 1979, Showers et al. 1995), mark-recapture data (Showers et al. 2001), apparent movement over bodies of water, sometimes associated with likely weather transport systems (Caffrey and Worthley 1927, Colenutt 1995, Bretherton and Chalmers-Hunt 1989, Langmaid and Young 2006), and population genetics studies (Martel et al. 2003) all indicate

that long-range movement of at least dozens of kilometers is possible for the European corn borer, but the frequency of and actual distances traversed during such movement are unknown.

In a previous study (Reardon et al. 2006), newly emerged marked adults dispersed at least 300 m, the longest distance within the sampling arena containing favorable aggregation site habitat. Others have noted a similar lack, or low level, of residency in many experiments involving release of newly emerged marked adults (Showers et al. 2001, Dalecky et al. 2006b). Reardon et al. (2006) suggested the possibility of an obligate migratory phase of young adults. Migration of many insects occurs during the prereproductive period (Johnson 1969, Drake et al. 1995, Dingle and Drake 2007). In this study, we used flight mills to test this hypothesis for European corn borer. Flight mill experiments obviously are behaviorally intrusive, and results such as distance flown and speed cannot be directly translated into behavior of adults under natural conditions (Dingle 1985, Gatehouse and Woodrow 1987, Sappington and Showers 1992b). Nevertheless, they are very useful for making relative comparisons of behavior between classes of insects, such as male versus female, mated versus unmated, and different ages, and provide insights sometimes unattainable in any other way (Sappington and Showers 1991, Cooter and Armes 1993, Dingle and Drake 2007). We hypothesized that if European corn borers have an obligate migratory behavior, it should manifest itself as a distinct age-related behavior. We also explored relative differences in flight behavior between sexes and between mating status, either of which could differentially affect age-related flight behavior.

Materials and Methods

Insect Culture. This study was conducted in 2006 and 2007 using adult European corn borers obtained from laboratory colonies at the USDA–ARS, Corn Insects and Crop Genetics Research Unit, Ames, IA. Colonies at this facility are established annually from wild females captured in central Iowa, and thus all experiments were conducted with adults from colonies less than a year in culture. Showers et al. (2001) concluded from mark-release studies that dispersal behavior of European corn borer males from a colony that had been in culture for 5 yr did not differ from males only one generation removed from the wild. Insects were reared following standard procedures (Guthrie et al. 1965) at 27°C, 16:8 (L:D), and 80% RH. Disease-free colonies were obtained by heat-treating the eggs (Raun 1961). Larvae were reared on a meridic wheat germ diet prepared according to Lewis and Lynch (1969), which contained Furidil B to inhibit microsporidial growth. Pupae were sexed and placed in separate emergence cages to prevent premature mating and were maintained under the same environmental conditions as the larvae.

Pupae were checked twice daily for emergence. Emerged adults were placed in sex-specific holding cages at 27°C, 16:8 (L:D), and 80% RH until they
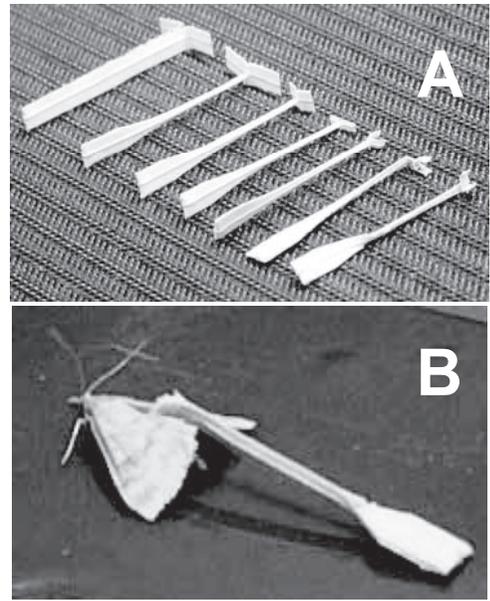

Fig. 1. (A) Progression from left to right of flight mill harness construction started by gluing two garden twist ties together for most of their lengths, followed by trimming and bending. (B) Tethered European corn borer female. The U-shaped harness is attached by superglue to the abdomen immediately posterior to the metathorax.

reached the appropriate age for flight tests or for mating. The holding cages consisted of a wire-mesh cylinder 13.5 cm in diameter and 15.5 cm tall and were placed on top of water-soaked cotton from which the adults could drink.

Adult Tethering. All experiments involved characterizing flight behavior of European corn borer adults on computer-interfaced flight mills. Adults were tethered to the mill with a harness design similar to that of Luo et al. (2002) but constructed from garden twist ties rather than copper wire (Dorhout 2007). The flat sides of two twist ties measuring 0.5 by 13 cm were glued together except at one end, which was separated to form a Y shape. Each harness was bent and trimmed to form a U-shaped end that allowed natural wing movement after attachment to the adult (Fig. 1A).

Each adult was sedated for ≈30 s by placing it for 8 s in a 100-ml plastic centrifuge tube containing 1 ml of ether applied to tissue paper (Luo et al. 2002, Wu et al. 2006). The U-shaped end of the harness was inverted and placed over the dorsum of the abdomen ≈2 mm behind the thorax (Fig. 1B). It was secured to the abdomen with a small amount of Insta-Cure+ glue (Bob Smith Industries, Atascadero, CA) at the base of the inverted U. The entire process took ≈45 s.

Flight Mills. The flight mill arm consisted of a triangle-shaped flat piece of aluminum (256 mm long, 160 mm from tip to pivot, 15 mm wide at base end) with an alligator clamp at the tip for attaching a harnessed adult perpendicular to the arm axis. A plastic sleeve mounted on the flight arm was slipped over a stationary central pin, and the arm was counter-bal-

anced with a moveable clip on the end opposite adult attachment. During flight, the adult flew in a horizontal plane, completing a circle of 1-m circumference per revolution about the central pin. Revolutions of the flight arm were sensed by an infrared eye mounted on the central post supporting the pin. Each flight mill was enclosed by a vinyl tent to reduce air flow around the adult and artifactual movement of the flight arm (Clark et al. 1984, Coats et al. 1986). Twelve (in 2006) or 16 (2007) flight mills were housed in a walk-in environmental chamber maintained at 24°C, 16:8 (L: D), and 80% RH. Adults were attached 3–4 h before the lights went off. Flight activity occasionally occurred before the lights went off or continued after they came back on at dawn. However, such flight was minimal, and it was unclear how to interpret such activity because the moths are nocturnal, so only flight data during the 8-h dark cycle were analyzed. The flight mills were connected to a Gateway 2000 personal computer by interface hardware and software as described by Beerwinkle et al. (1995).

Experiments. The first experiment tested the relative effects of adult age on flight performance of unmated adults on flight mills. Males and females were tested separately on given nights to prevent possible confounding effects of female sex pheromone. Adults that emerged during the night or early morning were categorized as 1 d old when flown on flight mills the following night. Dalecky et al. (2006b) found that European corn borer adults flew little on the night of emergence and behaved similarly to adults that emerged the following morning. Unmated adults were tested at 1, 2, 3, and 5 d of age.

The second experiment tested the flight performance of 2-, 3-, and 5-d-old females and 2- and 5-d-old males mated the previous night. Sexes were tested on different nights. In preparation for flight tests requiring mated females, unmated females of specified age were placed individually in small wire-mesh cages (8.5 cm diameter, 6 cm tall) on top of water-soaked cotton with two males of unspecified age and allowed one night to mate. Mating status of the female was confirmed after flight by dissecting its abdomen to check for a spermatophore (Showers et al. 1974b). In experiments requiring mated males, a single unmated male of specified age was placed in a cage with two virgin females of unspecified age and allowed one night to mate. Mating status of the male was confirmed before flight by dissecting both females to determine if one of them contained a spermatophore. If neither female contained a spermatophore, the male was discarded without testing.

Data Analysis. The number of revolutions was compiled for each flight mill in 1-min intervals. A given flight was considered terminated if an interval ≥1 min occurred without a recorded revolution of the flight arm. Adults that flew less than a cumulative total of 100 m during the night were excluded from the analyses. Although true nonfliers may have been eliminated in this way, it was considered preferable to including data from adults that were artifactually unable or indisposed to fly because of handling, the
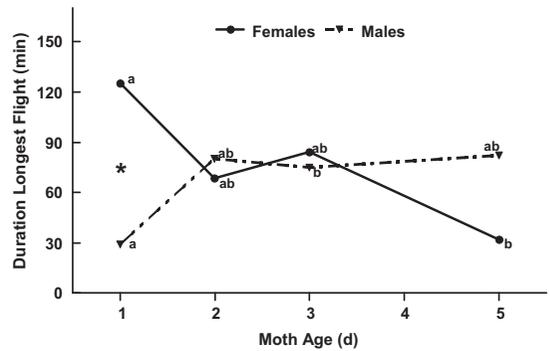

Fig. 2. Median duration of the longest-duration continuous flight of unmated male and female European corn borers of different ages during 8 h of darkness on laboratory flight mills. Sample sizes are the same as those in Table 1. Values within sex followed by the same letter are not significantly different ($\alpha = 0.05$; Kruskal-Wallis test). *Significant difference between males and females at indicated age ($\alpha = 0.05$; Wilcoxon rank sum test).

tethering process, or unknown causes unrelated to the variables being tested. Flight characteristics examined included duration of the longest single flight, distance of the longest single flight, average speed during the longest-duration flight, and total time spent in flight during the night.

All statistical tests were conducted using Statistix 7 software (Analytical Software 2000). Shapiro-Wilk normality tests (Royston 1995) indicated the data were not normally distributed, so nonparametric tests were used in all cases. Differences in flight characteristics among ages were examined with the Kruskal-Wallis one-way analysis of variance (ANOVA), with control of experimentwise error rate (Daniel 1990, Analytical Software 2000). Two-way comparisons between sexes or between mating status within a given age group were conducted with the Wilcoxon rank sum test (Daniel 1990, Analytical Software 2000). Differences in distribution were considered significant at $\alpha = 0.05$. Data are presented as medians. Medians are deemed to have more biological meaning than means in this case, because distributions of the data for flight parameters are all severely skewed.

Results

Unmated Adults. Duration of the longest single flight differed significantly with age for both unmated females (total $n = 178$, KW statistic = 9.045, $P = 0.029$) and unmated males (total $n = 162$, KW statistic = 8.164, $P = 0.043$). However, the patterns of change with age were different for the two sexes (Figs. 2 and 3). The median longest duration flight for unmated 1-d-old females was a little >2 h (125 min, $n = 42$), which was significantly greater than that of unmated 1-d-old males, which was only 29 min ($n = 47$; normal approximation = 4.08, $P < 0.0001$). Two of the unmated 1-d-old females tested flew continuously throughout the 8 h of darkness. About two thirds and one half of the unmated 1-d-old females made a con-
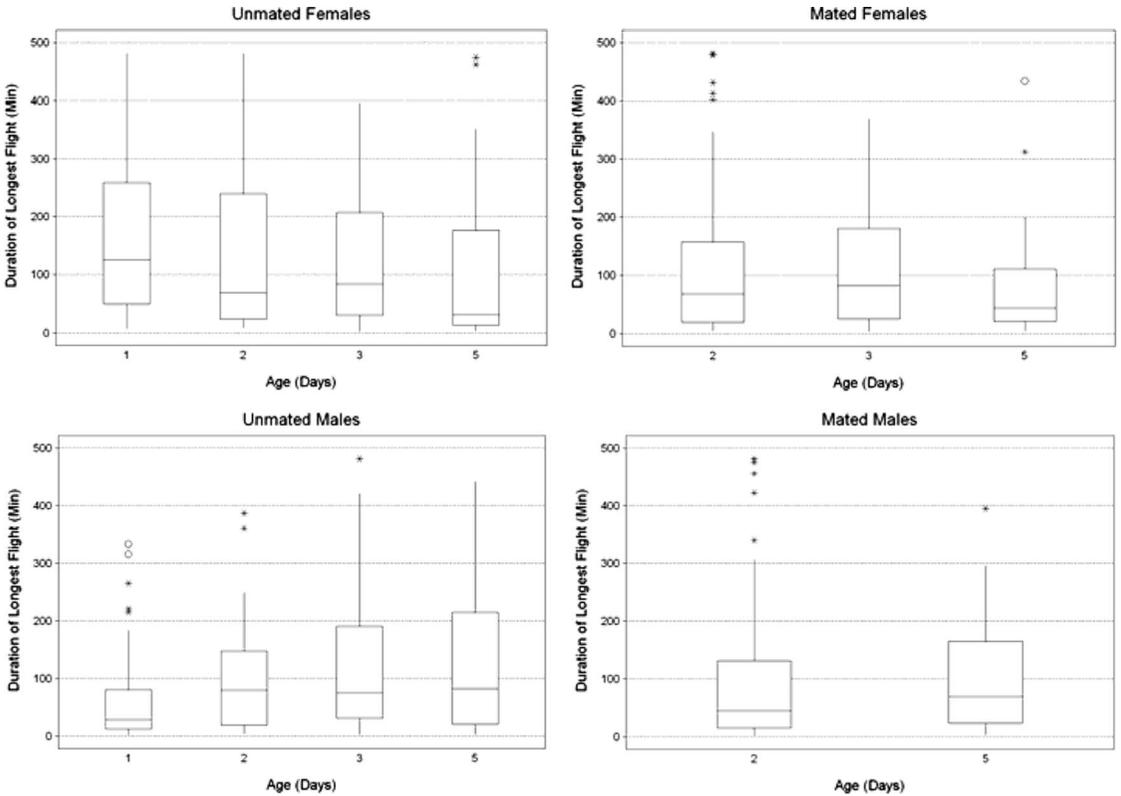
Fig. 3. Box and whisker plots (Analytical Software 2000) for the duration of the longest-duration continuous flight of unmated and mated male and female European corn borers of different ages during 8 h of darkness on laboratory flight mills. Sample sizes are the same as those in Table 1. Box encompasses middle half of data and is bisected by the median. Vertical lines (whiskers) indicate data within 1.5× the length of the box. Stars indicate data points >1.5× but ≤3× the length of the box. Circles indicate data points >3× the length of the box.

tinuous flight of at least 1 and 2 h, respectively (Fig. 4). In contrast, the longest flight by an unmated 1-d-old male was ≈5.5 h (333 min), and only about a third of the males tested made a continuous flight of even 1-h duration (Figs. 3 and 4).

Long-duration flight propensity of 2- and 3-d-old unmated females and males were similar, after decreasing and increasing, respectively, compared with that of 1-d-old adults (Fig. 2). Although the median longest duration flight of 5-d-old unmated females (32 min, $n = 45$) was significantly less than that of 1-d-old females, it did not differ significantly from the median longest duration flight of 5-d-old unmated males (82 min, $n = 36$; normal approximation = 1.725, $P = 0.085$), which remained similar to that of 2- and 3-d-old males (Fig. 2). The percentage of 1-d-old unmated females making continuous flights of minimum durations from 1 to 8 h was consistently greater than those of females of other ages (Fig. 4). In contrast, the percentage of 1- and 2-d-old unmated males making continuous flights of various minimum durations was consistently less than those of 3- and 5-d-old males.

Distance of the longest single flight by unmated females varied significantly with age (KW statistic = 10.47, $P = 0.02$; Table 1) in the same pattern as did duration of the longest duration flight (Fig. 2). The

same is numerically true for males, but the differences are not significant (KW statistic = 6.37, $P = 0.09$). The greatest distance flown in a single continuous flight by an unmated female during the 8 h of darkness was 25.1 km (2 d old) and for a male was 20.5 km (3 d old). Interestingly, the distance of the longest flight was significantly greater for unmated females than males for 1, 2, and 3 d olds (normal approximations = 5.40, 1.96, and 2.14; $P = 0.0001$, 0.050, and 0.033, respectively), even though this was not true of the duration of the longest flights (Fig. 2). The reason for this discrepancy is that 1-, 2-, and 3-d-old unmated females flew at speeds nearly twice that of unmated males of the same ages during their longest duration flight (normal approximations = 5.75, 3.00, and 4.47; $P = 0.0001$, 0.003, and 0.0001, respectively; Table 1). The greatest mean speed attained by an unmated female during the longest duration continuous flight was 1.09 m/s (1 d old) and for a male was 0.73 m/s (1 d old).

Total time engaged in flight activity of ≥1 min did not differ significantly with age for unmated females (KW statistic = 4.81, $P = 0.19$) but did differ significantly with age for unmated males (KW statistic = 10.83, $P = 0.01$), with 1 d olds flying significantly <3 d olds (Table 1). Total flight time did not differ significantly between males and females within age
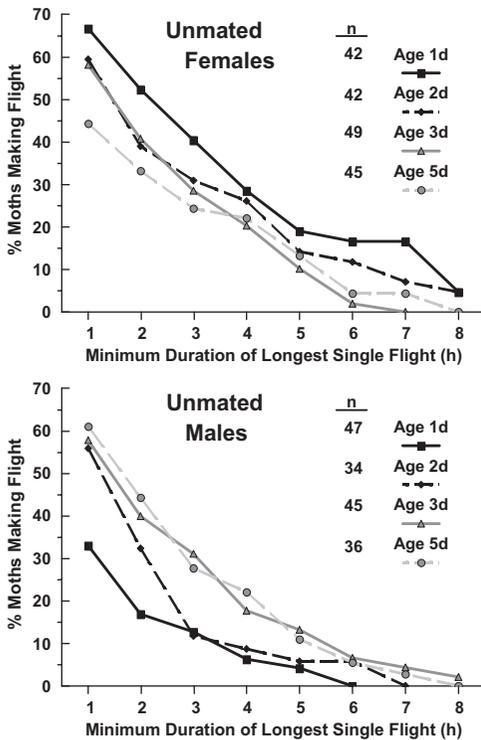
Fig. 4. Decumulation curves showing the percentage of unmated European corn borer adults of different ages engaging in continuous flights of indicated minimum durations.

classes, except that 1-d-old females flew significantly more total minutes than 1-d-old males (normal approximation = 4.163, $P < 0.0001$).

Mated Adults. Duration of the longest single flight did not differ significantly with age for either mated females (total $n = 118$, KW statistic = 1.45, $P = 0.48$) or mated males (total $n = 91$, KW statistic = 1.00, $P = 0.32$; Fig. 3). The same is true for all other flight parameters measured (Table 1). Furthermore, there were no significant differences between mated males

and females within age categories of 2 and 5 d, the only ages for which data from both sexes are available (Table 1), except that 2-d-old females flew faster than 2-d-old males (total $n = 87$, KW statistic = 4.59, $P = 0.03$). One or more adults of both sexes and all ages made a continuous flight >6 h (Fig. 3). One 2-d-old mated female and one 2-d-old mated male flew continuously through the 8 h of darkness (Fig. 3).

Comparison of Unmated and Mated Adults. There were no significant differences between mated and unmated adults of a given sex and age for any flight parameter (Fig. 3; Table 1). Patterns of changes in duration of the longest flight with age were very similar between mated and unmated adults of each sex (Fig. 3). Testing pooled data for mated and unmated females indicates the decrease in median flight duration between 3- and 5-d-old females is real (normal approximation = 1.99, $P = 0.046$; Figs. 2 and 3). Propensity to engage in long duration flight was similar between mated and unmated females of a particular age (Figs. 3 and 4).

Discussion

Distances covered by European corn borer adults during continuous flight on the flight mills was substantial, with medians mostly >1–2 km and some flying >20 km. However, drag from the weight of the flight arm and friction at the pivot make the distances and speeds measured in this study only minimum estimates of adult capability. Furthermore, wind can substantially increase the distance covered by dispersing insects in nature over that made possible by powered flight alone (Mikkola 1986, Drake and Farrow 1988, Johnson 1995, Pedgley et al. 1995, Gatehouse 1997, Srygley and Oliveira 2001, Dingle 2006), and there is evidence that European corn borer dispersal is affected by wind direction (Mikkola 1986, Showers et al. 1995, 2001). Showers et al. (2001) famously reported the fortuitous interception of a "swarm" of 10 or 11 European corn borers crossing a highway in front of a colleague's vehicle 100 min after a mass release of

Table 1. Median performance of unmated and mated European corn borer adults of different ages on laboratory flight mills during 8 h of darkness

Mating status	Age	No. analyzed (total tested)[a]		Total flight duration (min)[b]		Distance longest single flight (m)[b]		Speed during longest single flight (m/s)[b]	
		Female	Male	Female	Male	Female	Male	Female	Male
Unmated	1	42 (47)	47 (65)	355 a	162[d] a	3,143 a	456[d] a	0.52 a	0.26[d] a
	2	42 (45)	34 (57)	282 a	241 ab	1,845 ab	1,386[d] a	0.49 a	0.32[d] a
	3	49 (50)	45 (47)	284 a	281 b	2,428 ab	1,153[d] a	0.57 a	0.23[d] a
	5	45 (59)	36 (39)	261 a	249 ab	742 b	1,351 a	0.44 a	0.33 a
Mated[c]	2	41 (43)	46 (52)	267 a	231 a	1,071 a	1,249 a	0.43 a	0.34[d] a
	3	45 (63)	—	299 a	—	1,481 a	—	0.39 a	—
	5	32 (34)	54 (58)	223 a	242 a	605 a	1,163 a	0.36 a	0.32 a

There were no significant differences ($\alpha = 0.05$) between mated versus unmated within any age and sex categories.

[a] Moths that did not fly a cumulative total of at least 100 m during the 8 h of darkness were excluded from analysis to avoid artifactual bias caused by including individuals that may have been too damaged or traumatized during the tethering process to fly.

[b] Values within a column and of the same mating status followed by the same letter are not significantly different ($\alpha = 0.05$) (Kruskal-Wallis test).

[c] Individuals were flown the first full night after mating.

[d] Significant difference between males and females within a given age and mating status.

marked 1-d-old adults 14.2 km distant. Two females and one male hit the windshield, and all were marked. The adults were displaced in the direction of a light breeze (1.6–3.2 km/h), so their unaided flight speed was at least 1.47 m/s. This is substantially faster than the median (0.26 and 0.56 m/s), and maximum speeds (0.73 and 1.09 m/s) of unmated 1-d-old males and females, respectively, recorded during long flights on the flight mills.

For these reasons, flight duration is likely a better index of potential displacement of European corn borer adults than distance flown on the flight mills. Adults showed a remarkable capacity and propensity to make continuous flights >1 h in duration when tethered to laboratory flight mills. Although median duration of the longest flight was affected by age, some adults of all ages tested engaged in continuous flights of at least 5 h. Shirai (1998) examined flight behavior of the Asian corn borer, *Ostrinia furnacalis* Guenée, which circumstantial evidence suggests may be a migrant. The European corn borer is more divergent from the Asian corn borer than from some other *Ostrinia* species, but they are nevertheless closely related (Ishikawa et al. 1999, Frolov et al. 2007), as shown by a high rate of successful cross-species amplification of microsatellite loci (Coates et al. 2005, Dalecky et al. 2006a, Kim et al. 2008). Flight mill studies showed that the Asian corn borer is a strong flier, with ≈40% of unmated females 1–3 d old engaging in continuous flights of at least 6 h, dropping sharply by 4 d old (Shirai 1998). Males behaved similarly to females, except that propensity for long duration flight dropped after 2 d of age. Mean flight speed of 1-d-old unmated Asian corn borer females at 26°C was 0.55 m/s, very similar to the median speed of 0.52 m/s for 1-d-old unmated European corn borer females in our study. However, Asian corn borer males averaged flight speeds similar to females, unlike the case with European corn borers where male speed was much less.

Purposeful migration of female insects often coincides with the preoviposition period, a pattern originally referred to as the oogenesis flight syndrome (Johnson 1969). A more appropriate term to describe this pattern is migratory (or migration) syndrome (Drake et al. 1995, Dingle 2001, 2006, Dingle and Drake 2007, Roff and Fairbairn 2007), reflecting the species-specific integration of physiological, morphological, developmental, and behavioral mechanisms coordinating migration as a life history trait (Dingle 2006, Rankin 1989, Sappington and Showers 1992b, McNeil et al. 1995, Drake et al. 1995, Isaacs and Byrne 1998, Dingle and Drake 2007). Evidence from field studies has suggested that dispersal of European corn borers during the first full night after emergence is extensive, with only a small percentage remaining nearby for >1–2 d (Showers et al. 1976, 2001, Hunt et al. 2001, Qureshi et al. 2005, Sappington 2005, Dalecky et al. 2006b, Reardon et al. 2006). Females of this species do not call (i.e., release pheromone to attract males) on the night of emergence (Royer and McNeil 1991), but many mate the following night and most are mated by 2 d of age (Caffrey and Worthley 1927,

Royer and McNeil 1991, Fadamiro and Baker 1999, Dalecky et al. 2006b). However, the time needed for egg maturation results in a preoviposition period of 3–5 d (Caffrey and Worthley 1927, XiangQuan et al. 2004). Although highest for 1-d-old females, propensity and capacity for long-duration flight on the flight mills also was substantial for 2–3 d olds, declining significantly by 5 d of age. The age-specific pattern of long-duration flight observed in the laboratory suggests that the observed dispersal of newly emerged European corn borers in field studies is the result, in part, of an intrinsic tendency of 1-d-old females to engage in obligate migratory flight. This is not to say that all 1-d-old females will make a long migratory flight, because clearly some do not (Table 1; Figs. 3 and 4). Instead, migration is obligate for this group in the sense that when the behavior is expressed, its origins are intrinsic rather than the result of a facultative decision made in response to environmental conditions.

The situation with males may be different. One of the most intriguing patterns emerging from this study was the striking sex-specific difference in flight behavior of unmated 1-d-old adults, with duration of the longest flight being about four-fold less for males than females. Timing and extent of dispersal in males and females of migratory insect species sometimes differ, presumably in response to differential selection pressures impinging on the sexes (Johnson 1969, Baker 1978, Dingle 1985, Gatehouse and Zhang 1995, Denno et al. 2001). This may be the case with European corn borers, where there is no male equivalent of the female preoviposition period because spermatogenesis is complete by the time the adult emerges from the pupa (Chaudhury and Raun 1966). Although less than that of females, laboratory flight activity of 1-d-old males was still considerable, and seemingly enough to displace many of the marked adults in the above cited field studies beyond the arenas of attempted recapture. Nevertheless, the substantially lower propensity and duration of laboratory flights by 1-d-old males compared with that of females suggests that observed dispersal of males in the field may be caused by appetitive flight rather than true migratory behavior.

Timing of mating relative to migration is difficult to assess experimentally in insects and seems to depend on the species (Sappington and Showers 1992b, Gatehouse and Zhang 1995). The flight activity of mated adults on flight mills is sometimes less than that of unmated adults [e.g., *Helicoverpa armigera* (Hübner), Armes and Cooter 1991], but not always [e.g., *Agrotis ipsilon* (Hufnagel), Sappington and Showers 1992b]. Flight mill experiments with the Asian corn borer showed no differences in flight behavior of mated and unmated females, but mated males were less likely to engage in continuous long-duration flights than unmated males (Shirai 1998). Total flight activity and propensity to engage in long duration flights by European corn borers of either sex on the flight mills in our study was not affected by having mated the previous night. This is consistent with the results of previous mark-release experiments, where almost all Eu-

ropean corn borers released in grassy sites dispersed the first night, regardless of age, sex, or mating status (Reardon and Sappington 2007). Wild adults leave aggregation sites in large numbers soon after sunset each night (Showers et al. 1976, DeRozari et al. 1977, Sappington and Showers 1983a), weather conditions permitting, and nightly turnover of adults occupying grassy aggregation sites seems to be high (Bailey et al. 2007). Our results suggest that flight activity of adults of any age (at least up to 5 d), sex, or mating status is high, even if the behavior is not strictly migratory, which would lead to the observed high turnover in aggregation sites.

There are, of course, a number of limitations inherent in this kind of laboratory study. For example, given the large difference in flight behavior between 1-d-old unmated males and females, it would be of interest to examine flight of 1-d-old mated adults. However, most adults do not mate on the night of emergence (Royer and McNeil 1991, Fadamiro and Baker 1999), so this is likely not a major issue. However, it would be interesting to examine flight behavior on the same night as mating, but the logistics involved in obtaining adults that have just mated for tethering and flight during the same night would be formidable. Another major limitation to consider when interpreting the results is that, at the time of testing, the adults had not had an opportunity to engage in any previous flight activity except in a very limited space in a small holding cage. This is less of a concern when interpreting data for 1-d-old adults, because flight on the night or morning of emergence is limited (Dalecky et al. 2006a). Design of experiments to examine the effects of previous flight could provide important insights to European corn borer dispersal capacity in the field, and we are examining the feasibility of performing such experiments. Finally, we cannot rule out the presence of facultative migratory behavior in this species. Decisions to migrate may be influenced by environmental conditions experienced by larvae (Harrison 1980, Sappington and Showers 1992a, 1993, Hughes et al. 2004) or the adults themselves (Sappington and Showers 1993, Luo et al. 1995, Zhang et al. 2006). European corn borers have different numbers of generations per year depending on latitude (Showers et al. 1975, Showers 1979), and it is possible that expression of migratory behavior is influenced by a seasonal component.

Integrated Understanding of European Corn Borer Movement. Understanding European corn borer adult movement is critical for understanding this insect's population ecology, which in turn is critical to developing and assessing the viability of IRM strategies to protect the efficacy of *Bt*-transgenic corn. The rate of resistance evolution in a population and how fast resistance alleles will spread through the metapopulation depend both on how far adults move from their natal field and when mating occurs in relation to that movement. Despite intense study for many years, European corn borer movement, including its relation to mating, has proven very difficult to characterize. Part of this difficulty stems from the near-insurmountable obstacles to tracking the movements of an active noc-

turnal insect, which leads to the necessity of conducting experiments from which deductions about causal behavior must be drawn. Nevertheless, the combined efforts of many scientists over the years have led inexorably to significant advances and valuable insights. One of the cumulative effects of this research, however, has been to illuminate the complexity of behaviors underlying European corn borer adult movement. This alone has made progress difficult in attaining a holistic understanding of this species' movement and its consequences, because an unknown aspect of behavior can influence the results of an experiment, which may then render our interpretations and extrapolations inadequate.

In this context, a recent review of the principles of migration and animal movement by Dingle and Drake (2007) is very helpful in imposing order and synthesizing the variety of experimental results and observed behaviors in European corn borer. These authors point out that animal movement can be classified into three main types, all of which seem to be engaged in by European corn borer adults at different times and places during their adult life. The first is station keeping, which includes foraging behavior for resources, such as food, shelter, and mates. European corn borer males engage in foraging for mates, by casting for and following pheromone plumes released by calling females (Showers et al. 1974a, Roelofs et al. 1987). Mated females forage for oviposition sites, both for the preferred host plant (corn) (Bengtsson et al. 2006) and for preferred developmental stages of the host plant (Pilcher and Rice 2001). Both sexes search for free water in the form of dew droplets on vegetation to imbibe, which may be necessary before other behaviors are initiated such as those associated with mating (Showers et al. 1976, DeRozari et al. 1977). Movement associated with foraging behavior tends to be repetitive and meandering (Dingle and Drake 2007). Although net displacement of a foraging individual away from the original starting point can be considerable, it is relatively slight compared with the scale of displacement that would occur if flight over the same time period was directed in a straight line. A less common type of station keeping is commuting, where an individual makes regular round trips between patches of habitat which provide different resources (Dingle and Drake 2007). Interestingly, European corn borers may engage in this unusual behavior. At least some portion of the population, especially males and young females, occupy grassy aggregation sites in the daytime, but leave these sites at dusk to undertake other activities in other habitats such as the cornfield (Showers et al. 1976, Sappington et al. 1983a, b). Although it seems unlikely that individuals return to the same site each night (Bailey et al. 2007, Reardon and Sappington 2007), there is nevertheless a repetitive daily flux of movement into and out of aggregation sites at the population level.

The second type of movement (Dingle and Drake 2007) is called ranging, in which an individual moves beyond its current home range—i.e., the area it occupies when engaged only in station keeping move-

ment—in search of a resource unavailable in its current vicinity. Such movement is facultative and ceases when the resource is encountered (Jander 1975, Dingle and Drake 2007), after which station keeping behaviors resume. Hunt et al. (2001) concluded from mark-release experiments in Nebraska that spatial patterns of adult European corn borer movement can be affected by factors such as availability of suitable aggregation sites and hosts, as well as agronomic practices such as irrigation. Although adequate habitat usually is not limiting in most of the U.S. Corn Belt, ranging behavior by the adults may often be required to find suitable aggregation sites and cornfields in areas like the arid Great Plains (Lee 1988, Hunt et al. 2001, Qureshi et al. 2005). Even in Iowa where corn and grassy aggregation sites are abundant, adult daytime spatial distribution in the landscape changes as adults of the overwintered generation find and colonize grass adjacent to cornfields after emerging in fields rotated to soybeans (Sappington 2005).

The third type of movement discussed by Dingle and Drake (2007) is migration, which is characterized by roughly straight-line flight that is not interrupted by resource cues, such as suitable habitats or potential mates. Dispersal of newly emerged marked adults beyond suitable grassy aggregation sites (Showers et al. 2001, Reardon et al. 2006) is consistent with migratory behavior. However, such dispersal also is consistent with foraging behavior associated with goals unrelated to aggregation site colonization, having the effect of displacing the adults away from the adjacent available sites. The flight mill studies reported here suggest that it is indeed migratory behavior that disperses 1-d-old unmated females away from their emergence site. Male dispersal may instead be related to foraging for mates, although synthetic pheromone did not entice substantial numbers of newly emerged males to colonize grassy sites (Reardon et al. 2006). Migration can be obligate or facultative (Dingle and Drake 2007). The significant age-related pattern of flight behavior of European corn borer females on the flight mills suggests the behavior is intrinsic and therefore obligate. The flight mills indicate clearly that this behavior is differential, in that it differs between females and males, if males migrate at all. Furthermore, there is evidence that it may be partial migration, because not all 1-d-old females tested made long-duration flights. Likewise, even though most newly emerged marked European corn borer adults disperse soon after release, there are usually a few recovered nearby. The proportion recovered is often quite variable from test to test in the same location, suggesting that environmental factors like temperature, wind, or moisture influence expression of migratory and/or foraging behavior.

Although movement is a trait of an individual, cumulative movement by many individuals affects population-level phenomena (Dingle and Drake 2007). Most European corn borers in the Corn Belt engaging in migratory behavior will unavoidably begin and end their flights within the larger metapopulation. One consequence of migratory behavior in this species is dispersal of most females away from their natal field. Migration of this kind is not conspicuous, because the displacement takes place entirely within an area already occupied by other conspecifics. This is in contrast to species like the black cutworm, *Agrotis ipsilon,* which annually recolonizes areas far north of its overwintering range through migration in the spring (Showers 1997). Dispersal within a larger metapopulation does not result in a net change in population density in a given area but instead results in a spatial mixing or reshuffling of individuals within that area (Gandon and Michalakis 2001, Dingle and Drake 2007). Our flight mill results indicate not only that such spatial mixing of European corn borers is, in part, the result of an obligate migratory behavior of young females, but that the geographic extent of the resulting dispersal away from the natal site is well beyond the 800-m refuge maximum distance requirement and may be much greater than previously suspected.

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