Texas Is the Overwintering Source of Fall Armyworm in Central Pennsylvania: Implications for Migration Into the Northeastern United States

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ABSTRACT Fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), infestations in most of North America arise from annual migrations of populations that overwinter in southern Texas and Florida. *Cytochrome oxidase I* haplotype profiles within the fall armyworm corn strain, the subgroup that preferentially infests corn (*Zea mays* L.), can differentiate the Texas and Florida populations. We use this molecular metric to show that fall armyworms in central Pennsylvania originate from Texas, indicating the existence of a migratory pathway from Texas to the northeastern United States. These results were compared with historical trapping data for fall armyworm and another migratory noctuid, corn earworm *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), in the Pennsylvania and Maryland corn-producing areas to better define lepidopteran migratory pathways.

KEY WORDS *Spodoptera frugiperda*, cytochrome oxidase, Noctuidae, haplotype

The capacity for long distance migration often seen in the family Noctuidae has critical economic implications because it is a major mechanism for the seasonal expansion of pest populations. These species annually reinvade their northern geographic range, presumably to expand host resources, in spatial and temporal patterns that use dynamic but definable atmospheric pathways (Westbrook and Sparks 1986, Isard et al. 2005, Westbrook 2008). This is particularly true for species that do not diapause and therefore have a limited temperature range for overwintering. A notable example in North America is fall armyworm, *Spodoptera frugiperda* (J. E. Smith), a major pest of corn and other crops (Sparks 1979, Hall 1988, Pashley 1988a, Foster 1989). Populations that overwinter in southern Florida and Texas are responsible for annual infestations that extend throughout the central and eastern portions of the United States and southern Canada (Luginbill 1928).

Understanding the pattern of population movements is critical to efforts to control and predict infestations by migratory pests. Such knowledge makes possible a direct assessment of how conditions at the source location can influence the timing and severity of subsequent infestations and expedite identifying relationships that might have predictive value. An example of this is the positive correlation observed between corn acreage (the natal host resource) and the extent of subsequent fall armyworm infestation in cotton in adjacent states (Nagoshi 2009). The information will also facilitate the testing of aerobiological models designed to predict migratory movements (Isard et al. 2009).

Several attempts have been made to describe the annual migrations of fall armyworm in North America (reviewed in Nagoshi and Meagher 2008). The most detailed descriptions were inferred from the timing of fall armyworm appearances through trapping and other forms of monitoring (Luginbill 1928, Pair et al. 1986). These indicated both a northward movement from Texas into Oklahoma and a northeasterly flow from southern Texas that follows the Gulf of Mexico coastal plain into the Mississippi River Valley, with appearances in central Tennessee by mid-July, in southeastern Kansas in late July, and in the Ohio Valley and Maryland by August and September. Luginbill (1928) also suggested that populations in southern Florida migrate into north-central Georgia by June, continuing east of the Appalachians into South Carolina by July, and perhaps continuing northward along the Atlantic coastal plain. There may also be a northwesterly movement from southern Florida that contributes to the infestation in the Mississippi Valley (Pair et al. 1986). These descriptions are generally consistent with movements expected from average synoptic meteorological conditions (Rose et al. 1975, Westbrook and Sparks 1986, Mitchell et al. 1991) and the geographical distribution of subpopulations that

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differed with respect to disease or pesticide resistance (Young 1979, Fuxa 1987, Pitre 1988).

These approaches provide a broad picture of population movements but are limited in their resolution. In particular, inferences on the origin of immigrant populations become increasingly less accurate as migratory distance increases. Ultimately, the validation of projected pathways will require a direct method for identifying the overwintering origin, for example, by artificially tagging and recapturing immigrants or analysis of genetic or other physical markers that can distinguish between overwintering populations (see, for example, Showers et al. 1989, Hendrix and Showers 1992).

Fall armyworm can be subdivided into two behaviorally distinct, but morphologically identical, strains that were initially identified by differences in plant host distribution, hence their designation as rice strain and corn strain (Pashley et al. 1985, 1987; Pashley 1986, 1988b). Several studies have shown that polymorphisms in the mitochondrial *cytochrome oxidase I* (*COI*) gene provides a convenient and accurate marker for strain identity based on correlations with behavioral differences (Lu and Adang 1996, Levy et al. 2002, Meagher and Gallo-Meagher 2003, Prowell et al. 2004). The corn strain population as defined by the *COI* marker can be further subdivided into four haplotype subgroups designated as CS-h1, CS-h2, CS-h3, and CS-h4 (Nagoshi et al. 2007). Surveys of populations from Brazil, Texas, and Florida show that all four subgroups are present in each area, but there are consistent differences in their relative proportions. This is most evident when observing the ratio of the CS-h4 to CS-h2 haplotype proportions. Analysis of Florida corn strain populations over a 4-yr period and over several locations spanning the state showed a CS-h4/CS-h2 ratio that was consistently >1.0 (Nagoshi et al. 2007). In contrast, populations from Brazil and Texas, again sampled over multiple years and locations, consistently showed a ratio <0.5 (Nagoshi et al. 2007, 2008b). Because these haplotypes are defined by synonymous single nucleotide polymorphisms, it is reasonable to assume that they can serve as neutral markers to identify a Florida or Texas origin without the complications of selective pressure. As a proof of concept, corn strain populations in Georgia, Alabama, Louisiana, and Mississippi were analyzed for their CS-h4/CS-h2 ratios (Nagoshi et al. 2008b). These states lie along an east-west line from the Atlantic Ocean to the Gulf of Mexico and are north of the fall armyworm overwintering range. The results were consistent with the migratory pattern described by Luginbill (1928).

There were two objectives in this study. The first was to determine the source of the migratory fall armyworm populations in Pennsylvania. This state is a major corn producer that is located in an area that could be in the migratory path of both the Texas and Florida overwintering populations. The location of Pennsylvania, extending as it does from Lake Erie to the New Jersey border, is such that its population will likely be representative of the fall armyworm infesting most of the northeast section of the United States. The second objective was to determine whether the data from statewide trapping surveys can provide additional information about the direction of migration and the entry point into the state. The PestWatch program based at Pennsylvania State University makes available multiyear, statewide trapping data for fall armyworm (http://www.pestwatch.psu.edu/). This resource was used to compare the trapping patterns of fall armyworm with corn earworm, *Helicoverpa zea* (Boddie), another noctuid with an overlapping host range that also exhibits migratory flight behavior and nocturnal transport (Hendrix et al. 1987, Lingren et al. 1993, Westbrook et al. 1995, Westbrook et al. 1998). The implications of these observations on our understanding of fall armyworm migration and the usefulness of extensive historical pest survey data to investigate migration are discussed.

Table 1. Source locality information of fall armyworm collected from pheromone traps placed near corn fields

Label	Location	Date	Reference/collector
TX 04-6	Hidalgo Co, TX	2004–6	Nagoshi et al. 2008a, b
TX 06	San Angelo, TX	2006	Nagoshi et al. 2008b
TX 04	College Station, TX	2004	Nagoshi et al. 2008b
FL 02-3	Miami-Dade Co, FL	2002–3	Nagoshi et al. 2007
FL 04-5	Miami-Dade Co, FL	2004–5	Nagoshi et al. 2007
FL 06	FL (various sites)	2006	R.M.
PA 01	College Station, PA	2001	Fleischer et al. 2005
PA 06	Rock Springs, PA	2006	S.F.
PA 07	Rock Springs, PA	2007	S.F.

Materials and Methods

Specimen Collections and Sites. Fall armyworm specimens were obtained at several locations in the United States (Table 1). In the Florida collections from 2006 and 2007, adult males were collected using pheromone traps as previously described (Meagher 2001). Standard plastic Universal moth traps (Unitraps) were baited with a commercially available fall armyworm pheromone (Suterra, Bend, OR) and contained insecticide strips (Hercon Environmental, Emigsville, PA). After collection, specimens were typically stored at −20°C. In 2006 and 2007, the Pennsylvania samples were collected as above, using the "Fall Armyworm-PSU" lure (Scentry Biologicals, Billings, MT), which is the two-component lure described as Lure B that mitigates concern of nontarget captures in the northeast (Fleischer et al. 2005). In 2001, the Pennsylvania collections came from a subset of moths collected as described in Fleischer et al. (2005). The collected specimens were identified as fall armyworm by morphological criteria before molecular analysis.

Pheromone Trap Surveys. PestWatch is a regional interactive database for corn earworm, fall armyworm, and several other Lepidopteran pests organized and maintained by Pennsylvania State University (www.pestwatch.psu.edu) (Fleischer et al. 2007). In 2007, data from ≈660 sites in >20 states were provided by a wide array of agricultural scientists working in the public and private sectors. In Pennsylvania, these data

were provided primarily by Extension Educators who work with local vegetable producers and so the areas covered were focused where most sweet corn is produced. UniTraps were baited with the Fall Armyworm-PSU lure and species identification was performed on site (see www.ento.psu.edu/extension/factsheets/armyworm/idfallarmyworm.htm). The specimens collected were counted at 1-wk intervals, and the average daily catch rate was calculated with values rounded up to the nearest integer and recorded online.

In the survey of corn earworm, wire cone traps baited with pheromone lures specific to the species (Hercon Environmental) were monitored weekly, and the average daily capture rate was recorded online (listed as "Flight Activity"). In all cases, we were interested only in when the first captures occurred and not the number captured.

The Maryland data for corn earworm and fall armyworm were collected by the Maryland Department of Agriculture and were obtained from the website www.mda.state.md.us/plants-pests/plant_protection_weed_mgmt/plant_pest_survey_detection/interactive_map_links_daily_counts_at_individual_locations.php. Specimens in Maryland were examined by the Maryland Department of Agriculture to confirm species identity. In the Maryland survey of fall armyworm, traps were monitored at 6- to 8-d intervals in June and July and 7- to 22-d intervals afterward. Total trap captures per the trapping interval were recorded online.

DNA Preparation. Individual specimens were homogenized in 4 ml of phosphate-buffered saline (PBS; 20 mM sodium phosphate, 150 mM NaCl, pH 8.0) in a 15-ml test tube using a tissue homogenizer (PRO Scientific, Oxford, CT). Cells and tissue were pelleted by centrifugation at 6,000*g* for 5 min at room temperature. The pellet was resuspended in 800 μl cell lysis buffer (0.2 M sucrose, 0.1 M Tris-HCl, pH 8.0, 0.05 M EDTA, and 0.5% sodium dodecyl sulfate), transferred to a 1.5- or 2.0-ml microcentrifuge tube, and incubated at 55°C for 5 min. Proteins were precipitated by the addition of 100 μl of 8 M potassium acetate. The supernatant was transferred to a Zymo-Spin III column (Zymo Research, Orange, CA) and processed according to the manufacturer's instructions. The DNA preparation was increased to a final volume of 40 μl with distilled water. Each polymerase chain reaction (PCR) reaction required 1 μl of the DNA preparation ($\approx$0.02 μg).

PCR Analysis and Cloning. PCR amplification of the mitochondrial *COI* gene was performed in a 30-μl reaction mix containing 3 μl 10× manufacturer's reaction buffer, 1 μl 10 mM dNTP, 0.5 μl 20 μM primer mix, 1 μl DNA template (between 0.05 and 0.5 μg), and 0.5 U *Taq*DNA polymerase (New England Biolabs, Beverly, MA). The thermocycling program was 94°C (1 min), followed by 33 cycles of 92 (30 s), 56 (45 s), and 72°C (45 s), and a final segment of 72°C for 3 min. Typically 96 PCR amplifications were performed at the same time using either 0.2-ml tube strips or 96-well microtiter plates. Primers were synthesized by Integrated DNA Technologies (Coralville, IA). Amplification of the *COI* region used the primer pair *COI-893F* (5′-CACGAGCATATTTTACATCWGCA-3′) and *COI-1303R* (5′-CAGGATAGTCAGAATATCGACG-3′) to produce a 410-bp fragment.

Table 2. Strain proportions of fall armyworm analyzed from Centre Co., PA, traps in 2001, 2006, and 2007

Year	*n*	Corn strain	Rice strain
2001	170	0.81	0.19
2006	151	0.75	0.25
2007	182	0.86	0.14
	Average	0.81	0.19
Unpaired *t*-test (corn strain to rice strain)		$t = 13.64$	$P = 0.0002$

For fragment isolations, 6 μl of 6× gel loading buffer was added to each amplification reaction, and the entire sample was run on a 1.8% agarose horizontal gel containing GelRed (Biotium, Hayward, CA) in 0.5× Tris-borate buffer (TBE; 45 mM Tris base, 45 mM boric acid, 1 mM EDTA, pH 8.0). Fragments were visualized on a long-wave UV light box and cut out from the gel. Fragment isolation was performed using Zymo-Spin I columns (Zymo Research) according to the manufacturer's instructions. The isolated fragments were analyzed by DNA sequencing performed by Northwoods DNA (Bemidji, MN) or the University of Florida ICBR center. All other DNA sequences were obtained from NCBI GenBank. DNA comparisons, alignments, and restriction site mapping were performed using the DS Gene program (Accelrys, San Diego, CA).

Statistical Analysis. Corn acreage data were obtained from the National Agricultural Statistics Service (http://www.nass.usda.gov/).

Statistical analyses were performed using GraphPad InStat version 5.1 (GraphPad Software, San Diego, CA, www.graphpad.com). These include one-way analysis of variance (ANOVA) with a post hoc Tukey-Kramer multiple comparison test to compare haplotype ratio means and unpaired *t*-tests to compare strain frequencies in Pennsylvania pheromone trap collections.

Results

Fall Armyworm Haplotype Comparisons. Fall armyworm were collected by pheromone-baited traps in Pennsylvania in 2001, 2006, and 2007 and molecularly characterized for their *COI* haplotypes. In all 3 yr, >75% of the samples were of the corn strain as determined by the *COI* marker, consistent with the collections occurring in corn-dominated habitats (Table 2). A subset of the corn strain samples from each collection was analyzed for the proportions of the CS-h1, CS-h2, CS-h3, and CS-h4 haplotype groups, and from these data, the CS-h4/CS-h2 ratios were calculated (Fig. 1). For the 3 surveyed yr, the ratio averaged 0.23 ± 0.04 (SD). In comparison, the average ratios observed in Texas and Florida collections were 0.21 ± 0.06 and 3.01 ± 0.99, respectively. The means

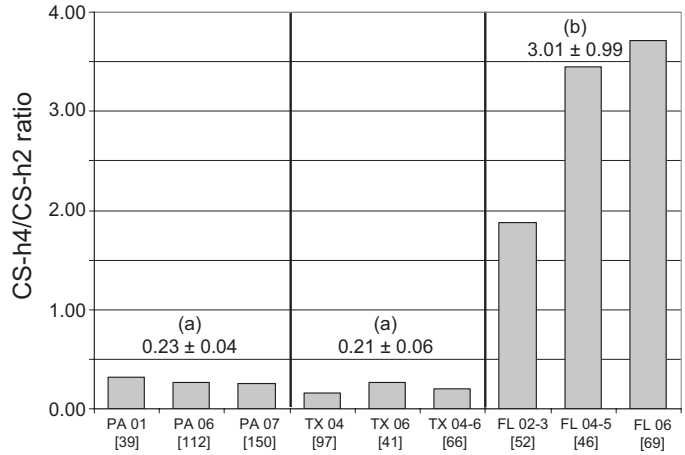


Fig. 1. CS-h4/CS-h2 ratios for corn strain samples analyzed in Pennsylvania, Florida, and Texas. Origin of samples are described in Table 1. Numbers in brackets indicate total number of samples. Numbers above bars represent mean ± SD. Different letters in parentheses indicate statistically significant difference ($P < 0.01$) from post hoc Tukey-Kramer multiple comparisons test ($q_{PA\text{-}TX} = 0.2$; $q_{PA\text{-}FL} = 8.3$; $q_{FL\text{-}TX} = 8.5$).

showed significantly different variation ($P = 0.0015$), with the Pennsylvania and Texas ratios indistinguishable from each other ($P > 0.05$) but each significantly different ($P < 0.01$) from the Florida populations. These results strongly suggest that Texas rather than Florida is the principle migratory source for the fall armyworm infesting Pennsylvania corn crops.

Comparison of Maryland and Pennsylvania Surveys. We were interested in determining whether state and regional trapping surveys could be used to confirm and refine the projected migratory pathways derived from molecular studies. Pheromone trapping data were publicly available for fall armyworm for Pennsylvania counties and selected regions in Maryland in 2008 (Table 3). We hypothesized that if migration along the east coast contributes significantly to the fall armyworm population in Pennsylvania, presumably occurring through a progressive northward establishment of populations, detection by pheromone trapping should consistently occur in Maryland before the more northern state of Pennsylvania. This was not the case. In both the Maryland Mid Shore and Lower Shore regions, the average date for the first fall armyworm capture was 1 and 4 July, respectively, with the earliest observation occurring in the collection period spanning days 171–177 (June 20–26). In comparison, fall armyworm was detected in Pennsylvania as early as days 159–165 (June 8–14), and the five earliest reporting Pennsylvania counties had positive collections from days 159–179 (June 8–28), with an average date of June 24.

Table 3. Collection periods of the earliest appearance of fall armyworm in pheromone traps located in selected counties of Maryland and Pennsylvania in 2008

State	County	Earliest appearance (DOY)
MD[a] (Mid Shore region)	Dorchester	171–177
	Queen Anne	178–183
	Caroline	178–183
	Talbot	184–191
	Average	184
MD[a] (Lower Shore region)	Wicomico	176–182
	Worcester	176–182
	Somerset	176–182
	Average	182
PA[b]	Schuylkill	159–165
	Franklin	166–172
	Blair	173–179
	Lebanon	173–179
	Lycoming	173–179
	Average	175

[a] Represents all regions for which trap data were available.
[b] Represents the five counties surveyed with the earliest detection date.
DOY, day of year.

This contrasts with the behavior of corn earworm, another migratory noctuid pest of corn. More extensive regional and multiyear pheromone trap surveys were available for corn earworm and are presented for the 2004–2008 period (Table 4). For each year, corn earworm was consistently observed in Maryland before Pennsylvania. There was on average a 34-d difference from the earliest Maryland report, typically from the Mid Shore region (day 128) and the first Pennsylvania observation that was usually from Schuylkill Co. (day 162).

Pennsylvania Trapping Data. The Pennsylvania-based Pestwatch program made it possible to map the timing of fall armyworm appearance in many of the major corn-growing counties in the state. Our simple expectation was that fall armyworm would tend to establish itself first in counties located early in the migration pathway and therefore the pattern of first detections could identify the entry point of the pest into the state. The timing of the first appearance in the surveyed counties was diagrammed for the 5-yr period from 2004 to 2008 (Fig. 2). A county was designated as "Early" if the first collection of fall armyworm was

Table 4. Collection periods (day of year) of the first appearance of corn earworm in regions of Maryland and counties of Pennsylvania

State	Region/county	2004	2005	2006	2007	2008	Average
MD[a]	Lower Shore	149–155	156–162	107–113	128–134	121–127	138
	Mid Shore	114–120	142–148	107–113	128–134	121–127	128
	Upper Shore	142–148	198–204	142–148	156–162	149–155	163
	Southern	177–183	156–162	107–113	135–141	121–127	145
	Baltimore-Harford	135–141	149–155	142–148	149–155	149–155	150
	Lower Central	135–141	149–155	135–141	135–141	135–141	143
	Central	163–169	156–162	135–141	135–141	135–141	150
	Western	163–169	156–162	149–155	135–141	149–155	156
PA[b]	Schuylkill	150–156	156–162	155–161	161–167	159–165	162
	Lancaster	157–163	170–176	152–158	154–160	159–165	166
	Bucks	192–198	156–162	155–161	154–160	159–165	169
	York	192–198	156–162	155–161	154–160	159–165	169
	Blair	178–184	163–169	152–158	154–160	173–179	172
	Centre	150–156	177–183	152–158	182–188	156–162	172
	Franklin	157–163	170–176	152–158	175–181	156–162	172
	Lycoming	192–198	170–176	148–154	161–167	180–186	176
	Indiana	171–177	184–190	152–158	168–174	180–186	179
	Lebanon	192–198	163–169	176–181	175–181	159–165	179
	Mifflin	157–163	170–176	176–181	182–188	180–186	179
	Dauphin	213–219	156–162	176–181	182–188	156–162	184
	Lehigh	206–212	163–169	155–161	189–194	257–263	199
	Luzerne	178–184	240–246	197–203	217–223	187–193	209
	Northampton	220–226	226–232	218–224	175–181	257–263	225

[a] Represents all regions for which corn earworm data were available.
[b] Represents all counties for which corn earworm data were available for all 5 yr.

within 2 wk of the initial observation within the state. Designations of "Middle" or "Late" were give to counties where the first detection of fall armyworm occurred at 3–4 wk after the initial state report, or later than 3–4 wk, respectively.

The pattern observed from year to year was highly variable, particularly with respect to the Early group (Fig. 2A). To identify locations where fall armyworm was consistently detected early, the average first detection time was calculated for those counties with at least 4 yr of trap data (Fig. 2B). Only two counties met the Early designation (Schuylkill and Lycoming), and these are more centrally located and nonadjacent. The three counties monitored with the highest corn acreage, Franklin, Lancaster, and York, are located on the southern border and were on average in the Middle group.

The corn earworm data again give a different result (Fig. 3). In this case, there was a bias for the Early first observations to occur more frequently in the eastern counties of Pennsylvania, particularly in 2005, 2006, and 2008, with 2004 being the sole exception. Early detection in the more western counties was sporadic. This becomes apparent in the map of the average appearance times where there is a clear clustering of Early designated counties in the southeastern portion of the state, suggesting that this is the likely entry point for the infesting population.

Discussion

Texas Origin of Pennsylvania Fall Armyworm. Analysis of the mitochondrial *COI* CS-h4/CS-h2 haplotype ratio showed that the majority of the fall armyworm infesting central Pennsylvania cornfields over a multiyear period descended from populations that overwintered in Texas. The close similarity of the Texas and Pennsylvania ratios strongly suggest limited, if any, mixing with migrants from Florida, although the possibility of a late season contribution cannot be precluded. These conclusions are consistent with the observation that, in 2008 (the only year where fall armyworm pheromone trapping surveys in Maryland were available), fall armyworm was detected in Pennsylvania before their first observation in the more southern state of Maryland. This suggests that, for at least 2008, contributions from a northward movement of fall armyworm along the eastern coast, an expected route of a Florida-based migration, were insignificant at the time of the Pennsylvania collections. Therefore, we conclude that migration from Texas through the Mississippi river valley is a primary source of fall armyworm populations in the northeastern portion of the United States, with perhaps only sporadic or late-season contributions from Florida populations.

These results have important ramifications. It means that fall armyworm infestations in most of North America will be influenced by agricultural practices in Texas that affect overwintering populations and the timing of migration. This would also be the case for any species that has similar migratory characteristics to fall armyworm, an important consideration when estimating the spread of exotic noctuid species or resistant lines that become established in this area. Studies are in progress to both confirm and extend the description of fall armyworm movements, including better defining the limits of the migrations from Florida and Texas and examining the meteorological, geographic, and biological factors that define the migratory pattern.

Using Trapping Surveys to Study Migration. In principle, publicly available historical trapping data in the Pennsylvania area could provide information about

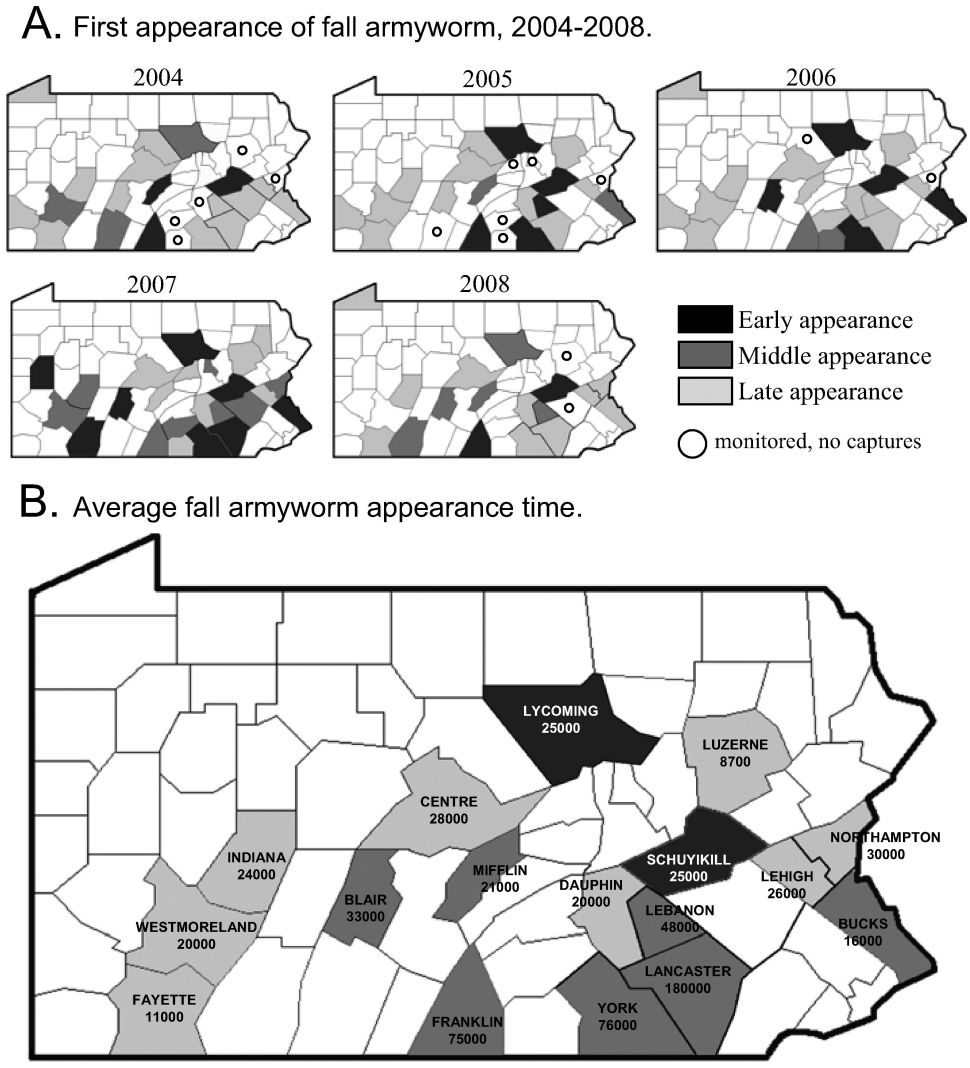
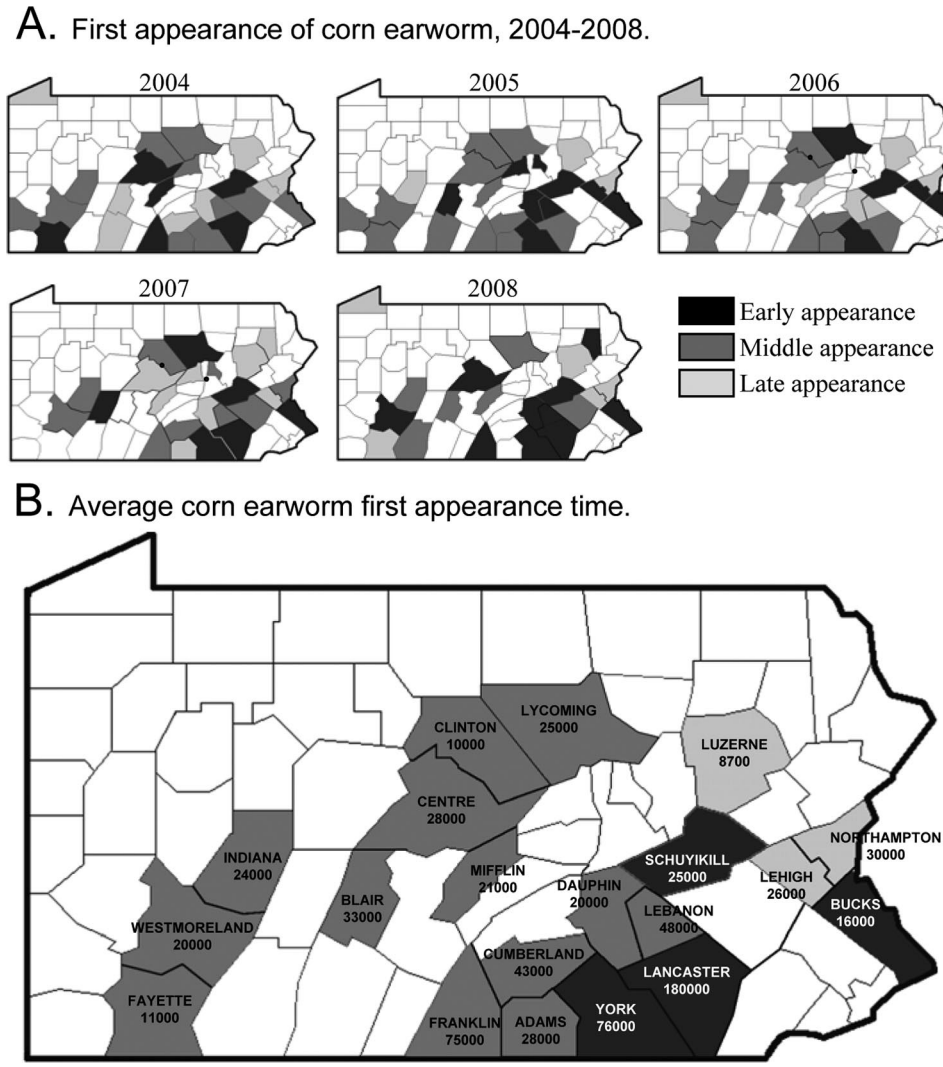


Fig. 2. Timing of the earliest detection of fall armyworm in Pennsylvania counties. The presence of fall armyworm was monitored by pheromone trapping. Early, fall armyworm collected within 2 wk of first report in the state; middle, fall armyworm detected 3–4 wk after the first report; late, earliest collection >4 wk after the first report. Unmarked counties were not monitored. (A) Year-to-year mapping of appearance time. (B) Average appearance time of counties with at least 4 yr of trapping observations from 2004 to 2008. Average acreage of corn planted in the monitored counties is given for the period 2004–2007 (2008 data not available) below county name.

the location and direction of migratory pathways. This is based on a simple premise: the timing of collections along a migratory pathway will reflect the movements of the population. If so, and if the migratory pathways are stable over time, there should be a clustering of early detection sites around the point of entry. This seems to be the case for corn earworm. Over a 5-yr period, the earliest detection of corn earworm in Pennsylvania tended to cluster in the southeast quadrant of the state, the surveyed region closest to the corn growing areas of Maryland (Fig. 3). When combined with their consistent detection in Maryland before Pennsylvania during this period (Table 4), the results suggest a northward entry of corn earworm into Pennsylvania occurring across the Maryland border.

In contrast, fall armyworm showed a more variable pattern from year to year, with no clear indication that a particular part of the state was more prone to the early arrival of this pest (Fig. 2). The interpretation of this result is problematic. Although systematic biases common to both collections (e.g., county-specific variations in corn acreage, pesticide use, timing, and accuracy of surveys) are unlikely because both the fall armyworm and corn earworm surveys were performed at the same times and locations, we cannot exclude the possibility of species-specific differences in the quality of the data collected. For example, if



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there are differences in the sensitivity or specificity of the pheromone trapping method used for each species, the different survey results could reflect variation in methodology rather than migratory behavior.

However, there are reasons to believe that the observed differences have a biological or ecological basis. Corn earworm differs from fall armyworm in its ability to diapause, thereby increasing its potential overwintering range to as far north as 40° N latitude (approximately the Maryland–Pennsylvania border). This range probably does not extend into Pennsylvania because viability is significantly reduced at temperatures below −1°C and attempts to overwinter corn earworm in the more southern states of Maryland and Virginia were unsuccessful (Horner et al. 2003). Therefore, like fall armyworm, virtually all the corn earworm infesting Pennsylvania is the result of immigration (Metcalf and Metcalf 1993, Diffenbaugh et al. 2008), but the distances from the nearest overwintering locations are much shorter. If variability in migration patterns increases with distance traveled, as would be expected, this could explain the more consistent patterns observed for corn earworm than fall armyworm with respect to initial detections in Pennsylvania and Maryland.

In summary, the use of mitochondrial haplotype comparisons provides a powerful method to identify the overwintering source of fall armyworm immigrants. From such information, it should be possible to delineate in detail the migratory pathways from south-

ern Texas and Florida to the rest of North America. Although, in principle, this methodology can be applied to any migratory species whose source populations have been reproductively isolated, the identification of appropriate diagnostic markers is not trivial, particularly in species where genetic characterization is limited. Given that, it is our hope that the migratory information obtained from fall armyworm will be applicable to other insects that likely have similar migratory behaviors but are less amenable to study. However, the limitation of this approach is shown by our preliminary observation that corn earworm and fall armyworm exhibit different patterns of immigration and establishment in Pennsylvania and surrounding areas. It indicates that the capacity to diapause and any resulting ecological interactions with transport probabilities must be considered before assuming comparable migratory patterns among different noctuid species. With this in mind, further work is ongoing to determine the natal sources of populations in the northeastern United States and along the eastern seaboard for both corn earworm and fall armyworm to confirm differences in migratory patterns, and if so, to identify the biological and ecological determinants.

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