

Multigenerational migration of fall armyworm, a pest insect

J. WESTBROOK ¹, † S. FLEISCHER,² S. JAIRAM,^{1,4} R. MEAGHER,³ AND R. NAGOSHI³

¹U.S. Department of Agriculture, Agricultural Research Service, College Station, Texas 77845 USA

²Pennsylvania State University, State College, Pennsylvania 16802 USA

³U.S. Department of Agriculture, Agricultural Research Service, Gainesville, Florida 32608 USA

Citation: Westbrook, J., S. Fleischer, S. Jairam, R. Meagher, and R. Nagoshi. 2019. Multigenerational migration of fall armyworm, a pest insect. *Ecosphere* 10(11):e02919. 10.1002/ecs2.2919

Abstract. Multigenerational insect migration commonly expands poleward, but meteorological influences are not clearly understood. We coupled biological and physical processes for the agricultural and invasive pest *Spodoptera frugiperda* (fall armyworm), by modeling its seasonal migration, and comparing simulated migrations to observed captures, and population genetic markers, at a continental scale. Simulations corroborated the spatial distribution and mixing of Texas and Florida source populations defined by genetic haplotypes. Positive relationships were found between first weeks of simulated and observed immigration, and between genetic and simulated metrics. The capacity to project biotic-, migratory-, and meteorology-induced shifts in insect distributions will aid strategic implementation of crop protection measures and economic analyses of host-resistant germplasm deployment in response to a warming climate.

Key words: aeroecology; fall armyworm; haplotype ratio; invasion; migration; pest; *Spodoptera frugiperda*.

Received 11 July 2019; revised 16 August 2019; accepted 3 September 2019; final version received 30 September 2019. Corresponding Editor: Robert R. Parmenter.

Copyright: © 2019 The Authors. This article has been contributed to by US Government employees and their work is in the public domain in the USA. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

⁴ Present address: Ingenium Schools, Monterey Park, California 91754 USA.

J. Westbrook: Retired.

† **E-mail:** jwestbrook49@gmail.com

INTRODUCTION

Migratory flight allows many insect species to rapidly expand their access to resources, which is critically important when local resources are inadequate or depleted (Drake and Gatehouse 1995, Chapman and Drake 2019). Migratory pest insects can abruptly invade and exploit new crop production regions before natural enemy populations increase or crop protection activities are performed. However, the timing and intensity of generational insect migrations and the associated influence of prevailing atmospheric factors are poorly understood. Such information will become increasingly relevant as changes in climate alter air transport systems and destabilize ecosystems, with unknown consequences to pest

migration patterns although poleward shifts of pest distributions have already been reported (Bebber et al. 2013).

Numerous species of insects engage in long-distance migrations that may require multiple generations (Drake 1985, Stefanescu et al. 2012). The aerial flux of migrating insects is profound, reaching 3200 tons of biomass over the southern UK annually (Hu et al. 2016), and displacements are linked to seasonally beneficial wind directions (Chapman et al. 2008, Wotton et al. 2019). Migrants find refuge, food resources, or reproductive habitat and may benefit by escaping predators and inadequate local resources (Drake and Gatehouse 1995). Further, migrant pests may convey genetic traits that provide tolerance to insecticides (Metcalfe 1989) and

plant-incorporated toxins (Storer et al. 2010, Tabashnik et al. 2013); may carry pathogens capable of infecting plants (Thresh 1989); and may directly injure plants by feeding (Dhaliwal et al. 2010). Coincidentally, beneficial arthropods (Weyman 1993), birds (Kelly et al. 2013), and bats (McCracken et al. 2008) are also known to migrate at high altitudes within the atmospheric boundary layer (Westbrook 2008) and may track the migration of pest insects to gain favorable prey resources.

Herbivorous migratory insects represent a type of migration that allows migrants to track available food resources (Chapman et al. 2004). Often migrations extend the insect population to geographic locations that are not sustainable for year-round survival, requiring migration back to refuge areas (e.g., winter-breeding regions; Westbrook 2008, Hu et al. 2016, Wotton et al. 2019). A critical difference between migrant and resident insects is in the pulsed nature of migrations and the timing of migrant interactions relative to host productivity (Bauer and Hoyer 2014). Pulses of migration allow migrants to quickly exploit ephemeral resources; irrigation and other crop production activities generally help migrants accomplish long-distance seasonal movements for which they might otherwise encounter large areas of unsuitable host resources. Productivity of both crops and non-cultivated plants is subject to climatic variability, which can impact the availability, growth stage, suitability, and geographic distribution of hosts on which migratory insects can feed and reproduce (Aragón and Lobo 2012, Shaw 2016).

Environmental conditions largely regulate the initiation and displacement of insect migrations. Populations of migratory insects may delay emigration flights if the wind speed is excessive. Further, precipitation or cool air temperature may inhibit emigration flights. Vertical stratification of air temperature, wind speed, or wind direction can lead to concentration of migrating insects into relatively thin altitudinal layers (Drake 1985, Drake and Reynolds 2012), in which the insects may be immersed in a low-level wind jet of high speed and favorable heading (for arriving at locations with advantageous resources). The development of low-level wind jets commonly occurs during the nocturnal period, when radiative cooling leads to

development of a temperature inversion in the atmospheric boundary layer that reduces the frictional effects of surface roughness on the wind velocity at the top of the atmospheric boundary layer (Bonner 1968, Westbrook and Eyster 2017).

Simulation trajectory and dispersion models have identified likely patterns of migration, but validation has been rare and typically limited to acute migration events for a single source or generation. Increased availability of atmospheric models, global atmospheric data, monitoring networks, and population genetics techniques (Kim et al. 2010, Nagoshi et al. 2012) now offer the means to both model and validate estimates of insect migration based on serial observations (e.g., trap collections) of insect distributions and genetic markers defining natal sources. New efforts are needed to simulate and validate insect migration models that span multiple sources and generations relative to a dynamic and heterogeneous host crop distribution (Stefanescu et al. 2012, Wang et al. 2019), dynamic meteorological processes, and to assess the relative local immigrant contribution of multiple source populations (Nagoshi et al. 2009).

We selected fall armyworm, *Spodoptera frugiperda* (J. E. Smith), as the migrant insect species for this study because it is a crop pest of tropical origin that cannot survive extended periods of freezing temperature (Sparks 1979). This means that winter-breeding populations of fall armyworm in the United States are historically found below 28° N latitude in southern portions of Texas and Florida, yet infestations during the subsequent local crop production period routinely extend as far north as Canada, a range approximating 3000 km (Mitchell et al. 1991). These observations reflect an annually recurring multigenerational migration behavior that we previously used to identify long-distance population movements (Westbrook et al. 2016). Expanding from this, multi-year simulations of multigenerational fall armyworm moth migration in North America were generated and tested by genetic and field-monitoring methods with the specific objectives to (1) identify seasonal and annual differences in migration patterns; (2) quantify the accuracy in estimating initial immigration; and (3) quantify the accuracy in estimating the mixing ratio of immigrants from two source populations.

METHODS

We compiled crop and moth development, moth migration simulation, trap capture, and genetic patterns to develop and validate a biophysical process defining multigenerational migration of corn-strain fall armyworm. Because of the lack of haplotypes distinguishing between source locations in the rice strain (RS), this paper is limited to corn-strain populations (the primary strain in corn [*Zea mays* L.] and sorghum [*Sorghum bicolor* (L.) Moench]). Migration was modeled in three phases, as previously detailed for one year (Westbrook et al. 2016), which are expanded here for four years and summarized below. The first phase created areas of identified field corn available for oviposition and development. We excluded sweet corn which is frequently treated with insecticides and would not produce significant numbers of fall armyworm moths, relative to field corn, at the scale of this study. A second phase accumulated degree-day values derived from air temperatures which were used to drive phenological development of corn, fall armyworm development and population dynamics, and plant–insect interactions used to define migratory propensity. In the third phase, we executed a migration simulation model by incorporating the distribution and growth stage of corn and the abundance of local and migratory fall armyworm moths within 1600-km² grid cells on a daily time step from 10 February to 31 December each year. Each year, simulation results of immigration timing were compared to independently observed trap captures, and simulation results expressing the dynamic geographic pattern of moth migration from two sources were compared to independently measured sources defined by haplotyping specimens from the trap captures.

Corn distribution

We downloaded corn planting distribution for 2011–2014 from the U.S. Department of Agriculture—National Agricultural Statistics Service CropScape—Cropland Data Layer (CDL; <http://nassgeodata.gmu.edu/CropScape/>; Han et al. 2012, 2014). Within an area of interest spanning 75° W to 105° W longitude, used to define corn production areas for potential infestation by immigrant fall armyworms (Fig. 1), CDL data were extracted in 40 km latitudinal bands. A total of

66 bands of the 30-m resolution CDL data were compiled, and the planted areas summed and upscaled into 1600-km² blocks for spatial compatibility with air temperature data used in simulations of corn growth, insect population development, and migration flights.

Development of corn plants and fall armyworms

We assumed that corn fields were planted on 15 February in the winter-breeding source areas of southern Texas (including Tamaulipas state in northeastern Mexico) and southern Florida and that initial infestation occurred at the 3–4 leaf stage, or 167 DD_{10°C} after planting, which is corroborated by the timing of larvae in two- to four-leaf corn in northern Tamaulipas, Mexico (Blanco et al. 2014). Corn plant and moth development calculations were driven by air temperature. Archived (40-km resolution) meteorological data from the Eta Data Assimilation System (EDAS) were downloaded from the USDC-NOAA Air Resources Laboratory (<http://www.ready.noaa.gov/archives.php>; Rolph 2013) to calculate cumulative degree-days that indicate the phenological growth stage of corn plants and fall armyworms. We projected the EDAS data (and CDL data) to latitude and longitude. We extracted (2 m above ground layer) air temperature data at 0600 Universal Coordinated Time (UTC) and 2100 UTC, representing approximate daily minima and maxima, respectively. Daily and cumulative degree-days (DD_{10°C} and DD_{13.8°C}), restricted to a maximum of 30°C for estimating corn plant growth, were calculated to simulate growth of field corn (Neild and Newman 1990) and fall armyworms (Hogg et al. 1982), respectively.

Simulating migration of fall armyworm moths

We simulated a total initial infestation of 1×10^6 fall armyworms in corn field source areas each year, comprised of 9×10^5 and 1×10^5 fall armyworms from southern Texas and southern Florida, respectively, accounting for differences in the respective total area of planted corn at similar infestation densities.

The propensity of migratory flight of *S. frugiperda* is poorly understood, but based on a related noctuid, corn earworm (*Helicoverpa zea*), we estimated newly eclosed fall armyworms to be as much as 30 times more likely to migrate from the silking stage than from the whorl stage

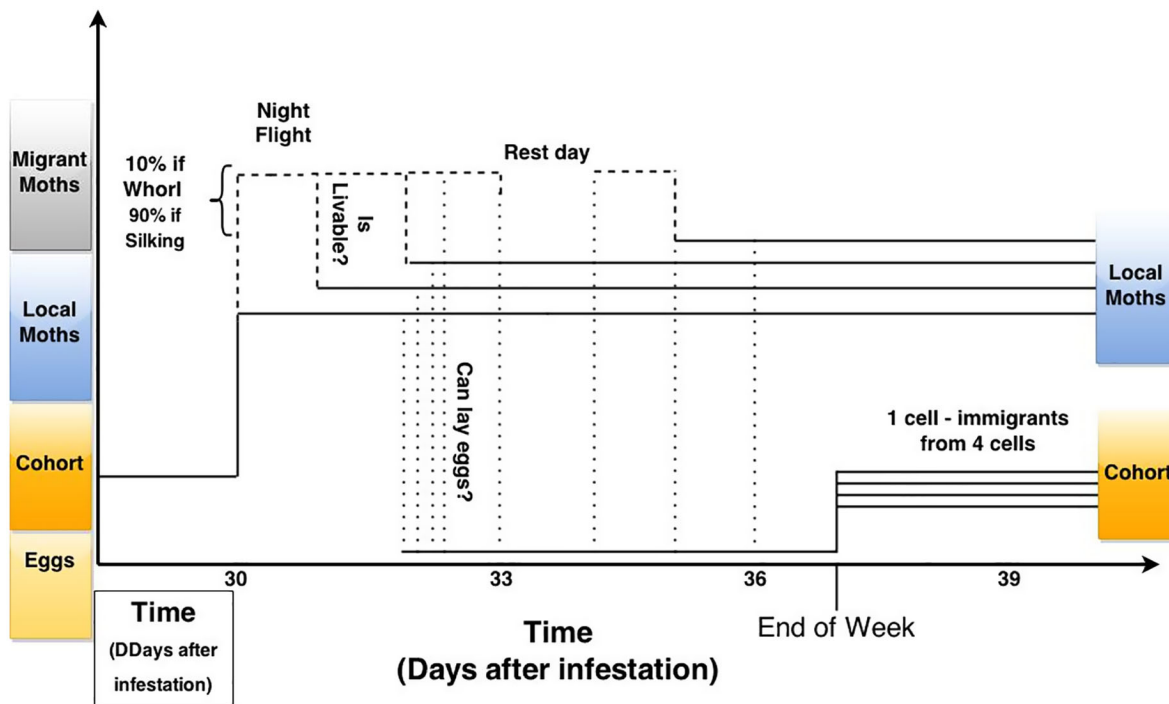


Fig. 1. Schematic representing local grid cell simulation of a fall armyworm cohort as it reaches adult emergence. The fraction entering migratory flight varies with the growth stage of corn. Moths that do not migrate remain in the cell of origin and contribute to the local moth population in that cell. Migratory moths entering that cell based on nightly atmospheric patterns also contribute to the local moth population in that cell. Moth retention and oviposition in a cell is dependent on corn phenology and can initiate a new cohort.

of corn (Westbrook and Lopez 2010). We assumed a ninefold variation in generational emigration of fall armyworm moths for all locations using an estimated proportion of 0.10 emigrants in moths that developed as larvae in whorl stage corn, and 0.90 emigrants in moths eclosing at the time of silking or later stage corn. The remnant (non-emigrant) proportion of moths (0.90 in whorl stage corn and 0.10 in silking stage corn) was identified as resident moths, which was restricted to local reproduction.

The EDAS meteorological data were input to the NOAA Air Resources Laboratory (ARL) HYbrid Single-Particle Lagrangian Integrated Trajectory (HYSPLIT) model (HYSPLIT PC version 4.9; Draxler and Hess 1998). Nightly emigration flights of fall armyworms were simulated from the HYSPLIT concentration model. We defined Pollutant Species in HYSPLIT as *TEX* (Specie 1) and *FLA* (Specie 2) for the Texas and Florida source populations, respectively. Although atmospheric deposition values were not defined per se,

we assigned dispersed moth values at the end of each nightly flight to respective grid cells for updating moth abundance and oviposition into susceptible corn fields. A point source emission file was defined to run emigration flights at 0000 UTC for a duration equal to the number of hours between sunset and sunrise (scotophase) minus 1 h and based on the nightly availability of migrant moths at each source location (i.e., grid cell). The emigrant portion of fall armyworm populations was translated to the emissions file exactly for each nightly flight. However, for the first emergence of the generation, we distributed the population of newly emerged moths over one week using an exponential decay function to simulate uncertainty in this event

$$E_i = E_t \times \left(e^{-\frac{i-1}{2}} - e^{-\frac{i}{2}} \right), \quad \text{for } i = 1 \text{ to } 7$$

where E is the number of emerged moths, and the subscripts i and t indicate day-of-week and total per weekly cohort, respectively. Further, we

assigned peak adult moth emergence of the first (F_1) generation on dates associated with the end of the week following a cumulative value of 346.2 DD_{13.8°C} (Hogg et al. 1982) after infestation. Peak moth emergence of the second (F_2) and third (F_3) generations was estimated to occur on dates associated with cumulative values of 692.4 DD_{13.8°C} and 1038.6 DD_{13.8°C} after initial infestation, respectively.

After nightly flights, moths were run through a biological model that linked to corn plant distribution and phenology. Migrants that terminated flight over large bodies of water or areas without corn were removed. We split the remaining population into resident moths and migratory moths for subsequent flights. We estimated the proportion of migrants depending on the suitability of corn plants in the area, which was associated with the crop growth stage based on cumulative DD_{10°C} within respective grid cells. Resident and migrant moths contributed to infestation contingent on this crop growth stage, but only moths that had not reached their ovipositional capacity contributed to the infestation. We pooled the number of fall armyworm larvae that developed from eggs during a specific week into a single cohort at the end of that week. Cohorts of immatures eclosed as adults (moths) after accumulating 346.2 DD_{13.8°C}. Subsequently, weekly patterns of simulated abundance of fall armyworm moths were estimated, retaining respective contributions from the *TEX* and *FLA* source areas.

Programs that executed the biological model and the HYSPLIT migration model were written in R (R x64 version 3.1.1; R Foundation for Statistical Computing, Vienna, Austria), Surfer (version 12.4.784; Golden Software, Golden, Colorado, USA), and MeteInfo (version 1.0.9.0; Wang 2014). Collection of one year of data required 70 h of computer processing time, 67 h of which were used to upscale the CDL data from 900 m² to 1600 km². The main program that executed the biological model and HYSPLIT model required 6 h to run a one-year simulation. We executed the moth migration model on an Intel Core 2 Quad CPU Q9650 3.00 GHz computer. Initial conditions for the biological model are the same as those noted in Westbrook et al. (2016). Meteorological model parameters have been revised slightly from those included in Westbrook et al. (2016): (1) Nocturnal migration

duration was changed from a fixed duration of 12 h to a variable duration (i.e., number of hours between sunrise and sunset minus 1 h) that accommodated seasonal and latitudinal effects; (2) *TEX* winter-breeding source population remained the same quantity but was distributed over a larger area (i.e., grid cells <28.5° N); and (3) *FLA* winter-breeding source population remained the same quantity but was distributed over a larger area (i.e., grid cells <28.5° N).

Comparing captured moths and simulated immigration

We compared weeks of first moth capture in pheromone traps with weeks of simulated first moth immigration. We selected pheromone trap data from the PestWatch database for locations with annual total capture ≥ 10 from UniTraps baited with sex pheromone (Appendix S1: Table S1) serviced once or twice weekly. We summarized, plotted, and analyzed weekly accumulations of simulated fall armyworm migration and total fall armyworm trap captures at each selected trap location using Grapher 11.4.770 (Golden Software, Golden, Colorado, USA), MapViewer 8.0.212 (Golden Software, Golden, Colorado, USA), and JMP 12.1.0 software (SAS Institute, Cary, North Carolina, USA). Due to the large data range and numerous zero values, data were logarithm-transformed (i.e., $\log_{10}(x + 1)$). We examined the ability of the model to explain variation in initial immigration using linear regression and a mixed model with year as a random variable and used paired t test to compare the first weeks of simulated immigration to first weeks of capture in traps. Further, natal source (*TEX* or *FLA*) attribution at sites with trap capture was estimated using the simulated moth migration data and parameterized as a migration index $[(\log_{10}(\text{FAW}_{\text{FL}} + 1) - \log_{10}(\text{FAW}_{\text{TX}} + 1)) / ((\log_{10}(\text{FAW}_{\text{FL}} + 1) + \log_{10}(\text{FAW}_{\text{TX}} + 1)))]$. The simulated migration index varies from -1 to $+1$, where negative values indicate higher contributions of the *TEX* natal origin and positive values indicate higher contributions of the *FLA* natal origin.

Determination of fall armyworm strain and haplotypes

Specimens were initially identified for strain by analysis of the mitochondrial gene cytochrome oxidase I (COI) *COI-891F/COI-1472R*

PCR amplification product. After polymerase chain reaction (PCR) amplification was completed, 5 units of the restriction enzyme EcoRV (New England Biolabs, Beverly, Massachusetts, USA) was added to each 20- μ L PCR mix along with 1 μ L of the manufacturer recommended 10 \times restriction enzyme buffer (final volume taken to 30 μ L with water). Restriction digests were incubated at 37°C 1–3 h. For each reaction, 6 μ L of 6 \times gel loading buffer was added and the entire sample run on a 1.8% agarose horizontal gel containing GelRed (per manufacturer's instructions; Biotium, Hayward, California, USA) in 0.5 \times Tris-borate buffer (45 mmol/L Tris base, 45 mmol/L boric acid, 1 mmol/L EDTA pH 8.0). Fragments were visualized on a long-wave UV light box. Only the RS-associated *COI* allele has an EcoRV site in the amplified region. Uncut fragments were preliminarily identified as corn strain (CS) and were cut out from the gel. Fragment isolation was performed using Zymo-Spin I columns (Zymo Research, Orange, California, USA) according to manufacturer's instructions. The isolated fragments were sequenced using primer *COI-891F* by the University of Florida Interdisciplinary Center for Biotechnology Research (UF-ICBR). DNA sequence comparisons were performed using Geneious version 5.6.2 created by Biomatters (<http://www.geneious.com/>). The h1-4 haplotypes were identified by the nucleotides found at *COI* sites 1164 and 1287 (Nagoshi et al. 2009). Each site was associated with two alternative bases to produce four possible haplotypes: h1 (A₁₁₆₄A₁₂₈₇), h2 (A₁₁₆₄G₁₂₈₇), h3 (G₁₁₆₄A₁₂₈₇), and h4 (G₁₁₆₄G₁₂₈₇). The frequencies of the four haplotypes were calculated for each collection, as was the quotient of the CS-h4 to CS-h2 frequencies, designated as the h4/h2 ratio.

Haplotype h4/h2 ratio data were calculated from collections of ≥ 15 captured fall armyworms during a week or pooled over several weeks for numerous locations (Appendix S1: Table S1). Haplotype ratio values defined the estimated source attribution of the local fall armyworm moth population. A haplotype ratio ≤ 0.5 defined the Texas source population; a value > 1.5 defined the Florida source population; and $0.5 < \text{value} \leq 1.5$ defined a Mixed source population (Nagoshi et al. 2012). To validate the migration model, the ability of simulated migration index

values to categorize source attributions defined by haplotype ratios was tested with logistic regression.

RESULTS

Insect and host plant growth

Corn planting dates (Appendix S1: Fig. S1) based primarily on long-term climatic data followed a northward gradient, but short-term, regional weather further modified geographic patterns of subsequent growth of corn plants within and between years. Climatic effects were reflected in the planting dates and acreage within a given year. Short-term, regional air temperature patterns directly influenced the pattern and growth rate of corn plants and fall armyworms. Further, short-term weather influenced the timing of fall armyworm eclosion (escape of the moth from the puparium), insect–plant interactions driven by physiological development of both crop and insect, propensity for migratory behavior, and ovipositional acceptance behavior, thus creating a dynamic, heterogeneous pattern of emigrant sources and immigrant establishment during the growing season (Fig. 1).

Insect migration flights

Migration patterns were simulated for four years, 2011–2014. Initial flight simulations began with the first projected emergence of adult fall armyworms in the winter-breeding areas, and subsequent migratory projections occurred following the emergence of successive generations of adult progeny in the winter-breeding areas and in areas of successful immigration and establishment. Moths were simulated to migrate at night at an initial flight altitude of 500 m above ground level.

Simulated migration of fall armyworms initially progressed northward from Texas and subsequently veered eastward into the Ohio River Valley as early as 30 June in 2011, 30 July in 2012 and 2014, or 10 September in 2013 (Fig. 2). Fall armyworms were simulated to migrate to the Canadian border of the United States by 10 September in 2011–2014.

The Florida winter-breeding population of fall armyworms was simulated to migrate by 10 May in 2011, 2013, and 2014 but not until 30 May in 2012 (Fig. 2). Simulated migration of the Florida

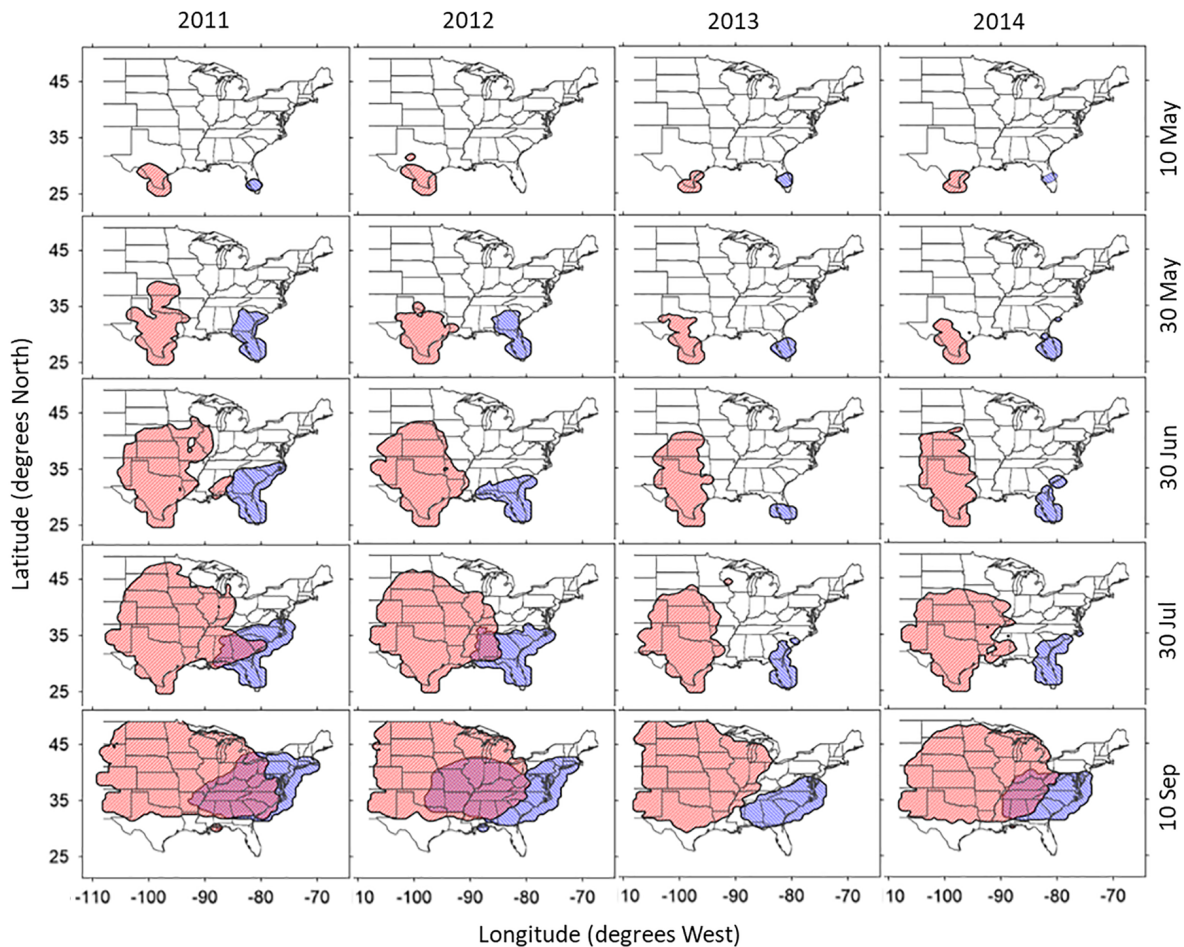


Fig. 2. Simulated fall armyworm moth migration (>500 moths per 1600 km²) from 10 May to 10 September 2011–2014. Colored contours represent Texas (red), Florida (blue), and mixed (purple) sources of immigrant fall armyworms.

population of fall armyworms advanced northward and along the mid-Atlantic coast of the United States. Aside from 2013, the Florida population of fall armyworms was simulated to migrate westward into the Mississippi River Valley by 30 July in 2011 and 2012 or 10 September in 2014.

The simulated first week of fall armyworm immigration increased from about Week 14 in Texas to greater than Week 34 in the northeastern United States in 2011–2014 (Fig. 3). Simulated first weeks of FAW immigration were regressed with observed weeks of first capture of ≥ 2 FAW in traps (county level), where ≥ 10 FAW were captured in a given year and no FAW were collected on the week of first trap inspection (Fig. 4). There

was a significant linear regression fit $FC = 18.93 + 0.31(SI)$, where FC is the week of first captured FAW and SI is the week of first simulated immigration ($F = 17.5$; $df = 1, 104$; $P < 0.0001$). The mixed model also showed a significant effect for trap capture ($P < 0.0001$) and an interaction with year ($P < 0.004$).

Simulated migration of moths from source populations in southern Texas and Florida resulted in varying ratios of the respective cohorts (Fig. 5). Simulated fall armyworms in the Plains states from Texas to North Dakota were exclusively from the Texas source population in 2011–2014. Although simulated fall armyworms from the Florida source population were predominant along the Atlantic coast of the UDS in

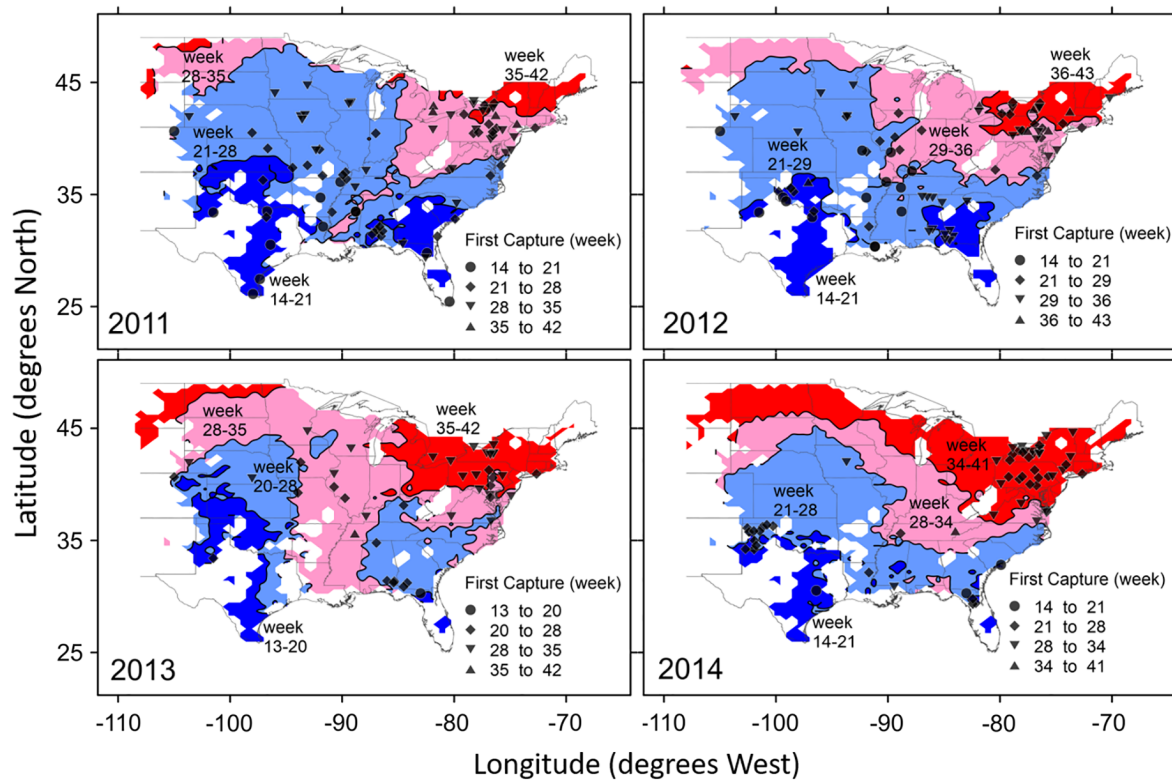


Fig. 3. Initial week of simulated immigration (shaded contour areas) and capture of fall armyworm moths from pheromone traps (symbols) in 2011–2014.

2011–2014, simulated fall armyworms from the Texas source population were found in the mid-Atlantic states in 2011, 2012, and 2014 but not in 2013. Simulated migration of fall armyworms from the Florida source population progressed to the eastern border of the Plains states, except in 2014 when simulated fall armyworms from the Florida source population were restricted to areas east of the Mississippi River Valley.

Genetic patterns supported the dynamic geographic patterns that emerged from the migration simulations (Fig. 6). Logistic regression showed that the probability of assignment of natal origin assignment based on haplotype ratio (Nagoshi et al. 2012) was strongly associated with a migration index derived from the moth migration simulations (see Appendix S1), which ranged from -1 to $+1$, where negative values indicate higher contributions of the TEX natal origin and positive values indicate higher contributions of the FLA natal origin (\log -likelihood $\chi^2 = 60.2$; $df = 2$; $P = 0.001$).

DISCUSSION

Simulated migratory flights were generated from short-term weather data, but resulting synoptic distributions revealed association with interannual climatic variability. Migratory flights were principally influenced by wind velocity (speed and direction) but were also directly linked with dynamic heterogeneity of emigrant sources driven by biological, meteorological, and behavioral factors. Incorporation of insect flight orientation could profoundly alter model simulations of individual flights (e.g., along an oceanic coastline) and generational migrations because flight orientation has been found to optimize seasonal migration displacements in several diurnal and nocturnal migratory insect species (Chapman et al. 2010).

There are several possible reasons for the limited fit between simulated immigration and capture of FAW in pheromone traps. One likely factor was practical limitations in monitoring

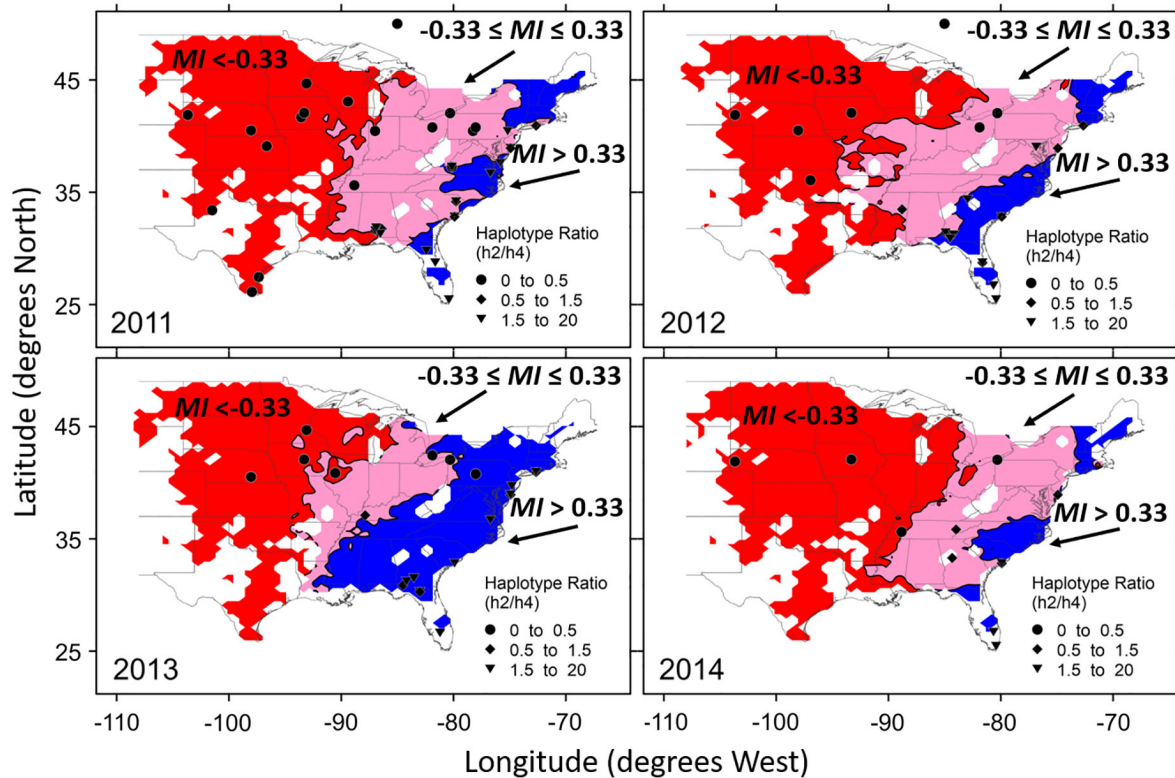


Fig. 4. Simulated migration index $((\log_{10}FL_{FAW} - \log_{10}TX_{FAW})/(\log_{10}FL_{FAW} + \log_{10}TX_{FAW}))$ of fall armyworm moth from populations that had originated in Texas and Florida (shaded contour areas) and observed haplotype ratio of captured moths (symbols) in 2011–2014. Migration index < -0.33 estimates Texas source; ≥ -0.33 and ≤ 0.33 estimates Mixed source; and ≥ 0.33 indicates Florida source. Haplotype ratio < 0.5 indicates Texas source; ≥ 0.5 and ≤ 1.5 indicate Mixed source; and ≥ 1.5 indicates Florida source.

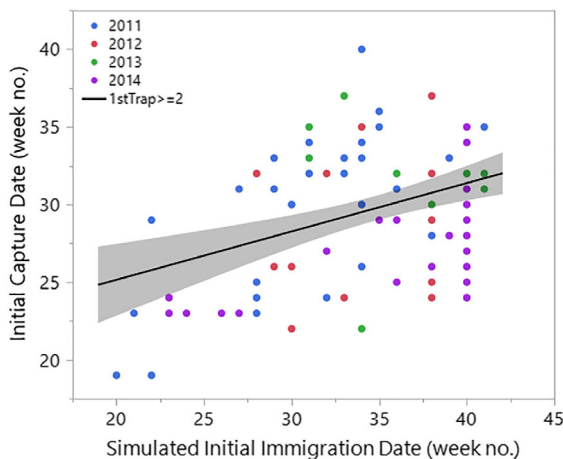


Fig. 5. Dates of simulated initial immigration vs. initial capture of fall armyworm moths in 2011–2014 ($Y = 18.93 + 0.3113 \times X$, $P < 0.001$, $R^2 = 0.144$).

range as years with more values across the full range of dates (2011 and 2014) showed a consistent positive relationship, whereas years with limited sampling (2012 and 2013) did not. Furthermore, pheromone traps attract only males at a stage receptive to a sex pheromone, which may not accurately reflect the timing, number, and geographic distribution of the total population. Methods that are not sex-biased and data with strong temporal and spatial resolutions would be ideal. There are also simplifying assumptions made in the model that could lead to inaccuracies. The current model did not incorporate flight speed or flight heading (crab angle relative to wind heading) and only incorporated field corn as a potential host plant. While corn is the primary host for the population of fall armyworm examined, significant contributions from other hosts are possible. It is also possible that

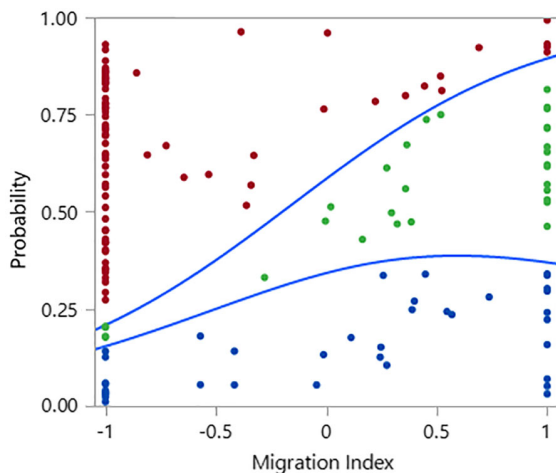


Fig. 6. Logistic regression showing probability of assignment of pheromone trap-captured fall armyworm moths from 148 sites in 2011–2014. Color indicates natal origin of moths captured in pheromone traps at that site and year as assigned by their haplotype ratios: blue—Florida, green—mixed, red—Texas. Data are aligned according to their simulated migration index values for that site and year, with the y position jittered randomly within the probability range for that migration index. Lines show nominal regression fits: Bottom line separates Florida from Mixed or Texas; top line separates Texas from Mixed or Florida. Distance between logistic regression lines and graph top or bottom gives estimates of the probability of being in a category along the migration index gradient.

winter-breeding FAW populations along mild Gulf coastal areas may have occurred farther north than the assumed northern limit (i.e., 28.5° N latitude; Garcia et al. 2018). In these locations, initial FAW captures would be from locally developed populations and not be indicative of a migration event.

Coupled biophysical air transport-based migration models have the potential to identify regions at risk for pests capable of long-distance flight and, in combination with future climate scenarios, project the consequences of climate change on pest migration. This will be particularly relevant to risk assessments involving the entry and establishment of invasive pest flying insects and the dispersal of newly arising alleles in endogenous pest populations. This is particularly relevant given the recent establishment of fall armyworm in Africa and its rapid spread

throughout that continent and in India (Day et al. 2017, Ganiger et al. 2018) and China (Li et al. 2019). Li et al. (2019) recently produced air transport-based model projections that supported the plausibility of annual fall armyworm migrations in Asia analogous to what is observed in North America. In this case, regions in Indochina and South China are projected to serve as overwintering sources for progressive waves of migration into eastern and northern Asia with the potential for substantial economic losses along the pathways. One notable distinction in their modeling is the assumption that fall armyworm will undergo three successive nocturnal flights, which differs from the variable number of flights, ranging from one to three, that are sufficient to describe the multigenerational migration observed in the United States. It will be interesting to see whether this difference is significant as it may indicate the conditions in Asia are less favorable for long-range migration than North America, which could mitigate the infestation risk. Efforts are underway in China to identify and introduce or augment natural enemy populations to reduce fall armyworm infestations (Silver 2019). Under such circumstances, migration models can inform conceptual designs for areawide or regional pest management programs by enabling estimates of the geographic potential of pest suppression that could be achieved with earlier pest suppression in smaller source regions. Specifically, interannual variability of flights and relative contributions of migrants from respective source areas may significantly impact the severity of pest infestations, and the mixing of genetic traits such as resistance to synthetic insecticides and insecticidal transgenic crops.

ACKNOWLEDGMENTS

T. M. O'Neil, T. Sappington, C. Livingston, R. Bowling, A. Peltier, B. R. Leonard, K. Estes, J. Obermeyer, G. Lorenz, B. McCornack, K. Tindall, A. Michel, T. Baute, P. Porter, J. S. Armstrong, E. Burkness, D. Cook, F. Musser, J. Knodel, J. Bradshaw, R. Wright, T. Hunt, T. Royer, R. Parker, A. Knutson, H. Stevens, E. Cullen, F. Peairs, J. Whalen, S. Menasha, J. Ingerson-Mahar, K. Holmstrom, T. Kuhar, A. Herbert, G. Dively, A. Muza, J. Timer, R. Pollack, T. Ford, R. Troyer, K. Watrous, A. Bachmann, C. Sidhu, C. Loveland, T. Abbey, T. Elkner, E. Swackhammer, K. Emfinger, and

T. Bailey assisted in trapping moths and reporting weekly moth capture data. USDC-NOAA provided access to HYSPLIT PC version 4.9 atmospheric transport modeling software. Mention of trade names or commercial products in this article is solely for the purposes of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture. USDA is an equal opportunity provider and employer. This material is based upon work that was supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, under award number 2011-67003-30209. JW, SF, RM, and RN conceived the ideas and designed methodology; JW, SF, RM, and RN collected the data; JW, SF, SJ, and RN analyzed the data; SJ developed and implemented the model; and JW, SF, SJ, RM, and RN led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. The authors declare no competing interests.

LITERATURE CITED

- Aragón, P., and J. M. Lobo. 2012. Predicted effect of climate change on the invasibility and distribution of the Western corn root-worm. *Agricultural and Forest Entomology* 14:13–18.
- Bauer, S., and B. J. Hoyer. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* 344:1242552.
- Bebber, D. P., M. A. T. Ramotowski, and S. J. Gurr. 2013. Crop pests and pathogens move polewards in a warming world. *Nature Climate Change* 3:985–988.
- Blanco, C. A., J. G. Pellegaud, U. Nava-Camberos, D. Lugo-Barrera, P. Vega-Aquino, J. Coello, A. P. Téran-Vargas, and J. Vargas-Camplis. 2014. Maize pests in Mexico and challenges for the adoption of integrated pest management programs. *Journal of Integrated Pest Management* 5:E1–E9.
- Bonner, W. A. 1968. Climatology of the low-level jet. *Monthly Weather Review* 96:833–850.
- Chapman, J. W., and V. A. Drake. 2019. Insect migration. Pages 573–580 in J. C. Choe, editor. *Encyclopedia of animal behavior*. Academic Press (Elsevier), Amsterdam, The Netherlands.
- Chapman, J. W., R. L. Nesbit, L. E. Burgin, D. R. Reynolds, A. D. Smith, D. R. Middleton, and J. K. Hill. 2010. Flight orientation behaviors promote optimal migration trajectories in high-flying insects. *Science* 327:682–685.
- Chapman, J. W., D. R. Reynolds, H. Mouritsen, J. K. Hill, J. R. Riley, D. Sivell, A. D. Smith, and I. P. Woitwod. 2008. Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Current Biology* 18:514–518.
- Chapman, J., D. Reynolds, and A. Smith. 2004. Migratory and foraging movements in beneficial insects: a review of radar monitoring and tracking methods. *International Journal of Pest Management* 50:225–232.
- Day, R. P., et al. 2017. Fall armyworm: impacts and implications for Africa. *Outlooks on Pest Management* 28:196–201.
- Dhaliwal, G. S., V. Jindal, and A. K. Dhawan. 2010. Insect pest problems and crop losses: changing trends. *Indian Journal of Ecology* 37:1–7.
- Drake, V. A. 1985. Radar observations of moths migrating in a nocturnal low-level jet. *Ecological Entomology* 10:259–266.
- Drake, V. A., and A. G. Gatehouse, editors. 1995. *Insect migration: tracking resources through space and time*. Cambridge University Press, Cambridge, UK.
- Drake, V. A., and D. R. Reynolds. 2012. *Radar entomology: observing insect flight and migration*. CABI, Oxfordshire, UK.
- Draxler, R. R., and G. D. Hess. 1998. An overview of the HYSPLIT_4 modeling system of trajectories, dispersion, and deposition. *Australian Meteorological Magazine* 47:295–308.
- Ganiger, P. C., H. M. Yeshwanth, K. Muralimohan, N. Vinay, A. R. V. Kumar, and K. Chandrashekara. 2018. Occurrence of the new invasive pest, fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae), in the maize fields of Karnataka, India. *Current Science* 115:621–623.
- Garcia, A. C., W. A. C. Godoy, J. M. G. Thomas, R. N. Nagoshi, and R. L. Meagher. 2018. Delimiting strategic zones for the development of fall armyworm (Lepidoptera: Noctuidae) on corn in the state of Florida. *Journal of Economic Entomology* 111:120–126.
- Han, W., Z. Yang, L. Di, and R. Mueller. 2012. CropScape: a Web service based application for exploring and disseminating US conterminous geospatial cropland data products for decision support. *Computers and Electronics in Agriculture* 84:111–123.
- Han, W., Z. Yang, L. Di, A. L. Yagci, and S. Han. 2014. Making cropland data layer data accessible and actionable in GIS education. *Journal of Geography* 113:129–138.
- Hogg, D. B., H. N. Pitre, and R. E. Anderson. 1982. Assessment of early-season phenology of the fall armyworm (Lepidoptera, Noctuidae) in Mississippi. *Environmental Entomology* 11:705–710.
- Hu, G., K. S. Lim, N. Horvitz, S. J. Clark, D. R. Reynolds, N. Sapir, and J. W. Chapman. 2016. Mass seasonal bioflows of high-flying insect migrants. *Science* 354:1584–1587.
- Kelly, J. F., E. S. Bridge, W. F. Frick, and P. B. Chilson. 2013. Ecological energetics of an abundant aerial

- insectivore, the purple martin. *PLOS ONE* 8: e76616.
- Kim, K. S., G. D. Jones, J. K. Westbrook, and T. W. Sappington. 2010. Multidisciplinary fingerprints: forensic reconstruction of an insect reinvasion. *Journal of the Royal Society Interface* 7:677–686.
- Li, X., et al. 2019. Prediction of migratory routes of the invasive fall armyworm in eastern China using a trajectory analytical approach. *Pest Management Science*. <https://doi.org/10.1002/ps.5530>
- McCracken, G. F., E. H. Gillam, J. K. Westbrook, Y.-F. Lee, M. L. Jensen, and B. B. Balsley. 2008. Brazilian free-tailed bats (*Tadarida brasiliensis*: Molossidae, Chiroptera) at high altitude: links to migratory insect populations. *Integrative and Comparative Biology* 48:107–118.
- Metcalfe, R. L. 1989. Insect resistance to insecticides. *Pest Management Science* 26:333–358.
- Mitchell, E. R., J. N. McNeil, J. K. Westbrook, J. F. Silvain, B. Lalanne-Cassou, R. B. Chalfant, S. D. Pair, V. H. Waddill, A. Sotomayor-Rios, and F. I. Proshold. 1991. Seasonal periodicity of fall armyworm, (Lepidoptera: Noctuidae) in the Caribbean basin and northward to Canada. *Journal of Entomological Science* 26:39–50.
- Nagoshi, R. N., S. J. Fleischer, and R. L. Meagher. 2009. Texas is the overwintering source of fall armyworm in central Pennsylvania: implications for migration into the northeastern United States. *Environmental Entomology* 38:1546–1554.
- Nagoshi, R. N., R. L. Meagher, and M. Hay-Roe. 2012. Inferring the annual migration patterns of fall armyworm (Lepidoptera: Noctuidae) in the United States from mitochondrial haplotypes. *Ecology and Evolution* 2:1458–1467.
- Neild, R. E., and J. E. Newman. 1990. Growing season characteristics and requirements in the Corn Belt. National Corn Handbook NCH-40. Purdue University, West Lafayette, Indiana, USA.
- Rolph, G. D. 2013. Real-time Environmental Applications and Display sYstem (READY) Website (<http://ready.arl.noaa.gov>). NOAA Air Resources Laboratory, Silver Spring, Maryland, USA.
- Shaw, A. K. 2016. Drivers of animal migration and implications in changing environments. *Evolutionary Ecology* 30:991–1007.
- Silver, A. 2019. Caterpillar's march across China spurs hunt for native predator. *Nature* 570:286–287.
- Sparks, A. N. 1979. A review of the biology of the fall armyworm. *Florida Entomologist* 62:82–86.
- Stefanescu, C., et al. 2012. Multi-generational long-distance migration of insects: studying the painted lady butterfly in the Western Palearctic. *Ecography* 35:001–014.
- Storer, N. P., J. M. Babcock, M. Schlenz, T. Meade, G. D. Thompson, J. W. Bing, and R. M. Huckaba. 2010. Discovery and characterization of field resistance to Bt maize: *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Puerto Rico. *Journal of Economic Entomology* 103:1031–1038.
- Tabashnik, B. E., T. Brévault, and Y. Carrière. 2013. Insect resistance to Bt crops: lessons from the first billion acres. *Nature Biotechnology* 31:510–521.
- Thresh, J. M. 1989. Insect-borne viruses of rice and the Green Revolution. *Tropical Pest Management* 35:264–272.
- Wang, Y. Q. 2014. MeteoInfo: GIS software for meteorological data visualization and analysis. *Meteorological Applications* 21:360–368.
- Wang, H.-H., W. E. Grant, N. C. Elliott, M. J. Brewer, T. E. Koralewski, J. K. Westbrook, T. M. Alves, and G. A. Sword. 2019. Integrated modelling of the life cycle and aeroecology of wind-borne pests in temporally-variable spatially-heterogeneous environment. *Ecological Modelling* 399:23–38.
- Westbrook, J. K. 2008. Noctuid migration in Texas within the nocturnal aeroecological boundary layer. *Integrative and Comparative Biology* 48:99–106.
- Westbrook, J. K., and R. S. Eyster. 2017. Atmospheric environment associated with animal flight. Pages 13–45 in P. Chilson, W. Frick, J. Kelly, and F. Liechti, editors. *Aeroecology*. Springer, New York, New York, USA.
- Westbrook, J. K., and J. Lopez. 2010. Long distance migration in *Helicoverpa zea*: what we know and need to know. *Southwestern Entomologist* 35:355–360.
- Westbrook, J. K., R. N. Nagoshi, R. L. Meagher Jr., S. J. Fleischer, and S. Jairam. 2016. Modeling seasonal migration of fall armyworm moths. *International Journal of Biometeorology* 60:255–267.
- Weyman, G. S. 1993. A review of the possible causative factors and significance of ballooning in spiders. *Ethology, Ecology and Evolution* 5:279–291.
- Wotton, K. R., B. Gao, M. H. M. Menz, R. K. A. Morris, S. G. Ball, K. S. Lim, D. R. Reynolds, G. Hu, and J. W. Chapman. 2019. Mass seasonal migrations of hoverflies provide extensive pollination and crop protection services. *Current Biology* 29:2167–2173.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2919/full>