Noctuid migration in Texas within the nocturnal aeroecological boundary layer

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Synopsis

Long-distance migration of adult corn earworm moths (Helicoverpa zea), and several other noctuid moth species, facilitates seasonal expansion of pest populations and consequent increased infestations of agricultural crops on a continental scale in North America. Long-term field studies of population dynamics and migratory flights of H. zea and fall armyworm (Spodoptera frugiperda) in the United States were evaluated using X-band radar observations and profiles of atmospheric conditions. These studies identified characteristic patterns of migratory flight that are largely associated with vertical profiles of temperature and wind speed. Collective patterns of moth migrations were generally highly correlated with wind headings, but often at a significant angular deviation. Preliminary analyses are presented between moth distributions in the aerosphere estimated from discrete moth counts using X-band radar and bulk reflectivity data from NEXRAD Doppler radar. Identification of associations between atmospheric factors and noctuid population dynamics and migratory flights will improve the ability to predict infestations by pest species throughout their broad seasonal range expansion.

Introduction

The corn earworm (Lepidoptera: Noctuidae) is a major economic pest of field crops and vegetables in the United States (US). Corn earworms (Helicoverpa zea) are polyphagous and infest cotton, sorghum and other crops, but corn appears to be a favored host for reproduction. Several generations of H. zea are common in the continental US. H. zea has a capability to diapause, which allows the pest to overwinter as a pupa in the soil at locations where freezing temperatures rarely occur if at all. The flight capability of H. zea, which is a facultative migrant, contributes significantly to its pest status (Fitt 1989) and is the principal subject of this article.

X-band radar studies of noctuid migratory flight were conducted in the Lower Rio Grande Valley (LRGV) of Texas and Mexico where 200,000 ha of irrigated corn were grown. Excavation of pupae from the soil in corn fields identified H. zea and the fall armyworm (Spodoptera frugiperda), an obligate migrant, as the predominant noctuid pests (Raulston et al. 1992). A single generation of adult H. zea and S. frugiperda emerged during annual US Department of Agriculture (USDA) noctuid migration studies in June (Pair et al. 1991; Raulston et al. 1995). Observations by night vision revealed that H. zea and S. frugiperda were the predominant flying insects of this size. Further, these noctuid species have radar cross-sections that are consistent with the maximum range of individual H. zea and S. frugiperda detected by X-band radar (Wolf et al. 1993).

The purpose of this article is to attribute the value of radar to studies of long-distance, high-altitude migration flights of noctuids, several of which are important crop pest insects. The article outlines characteristics of migratory flight behavior that have been obtained through extensive field radar entomological measurements coupled with high-altitude atmospheric measurements. The summary of information fills knowledge gaps about noctuid migration, and will contribute to the development of pest management strategies that account for the timing and abundance of migration events. Further, continued development and implementation of radars may extend their value for aeroecological monitoring of the seasonal dispersal of a broad range of species.

Observational methods

Because H. zea and other noctuid pests are nocturnally active, observation and identification of flying noctuids becomes challenging. Further, noctuids often fly at altitudes beyond the view of a ground observer. Several general approaches have
been used to monitor noctuid flight: visual observation and imaging, aerial collections, and radar.

Visual observation and identification have been used effectively to monitor local dispersal flight and take-off ascent flight. Experienced observers have used night vision image intensifiers with and without infrared illumination to examine noctuid dispersal within and between local habitats (Lingren 1978). The night vision technique has permitted observation of noctuids as high as 100 m above ground level (AGL). Image recording devices have improved significantly in terms of cost and technical characteristics (resolution, speed, recording capacity, size, weight, and infrared sensitivity).

Efforts to confirm the presence of *H. zea* and other noctuids above 100 m AGL have been made using light traps on a radio tower (Callahan et al. 1972) and aerial nets attached to tethered kites, airplanes (Glick and Noble 1961; SD Pair, unpublished; WW Wolf, unpublished; KR Beerwinkle, unpublished), and helicopters (Beerwinkle et al. 1989). Collection of noctuids by the use of aerial nets has been limited by relatively low sampling volumes. Aerial netting, however, has confirmed the presence of *H. zea* and other noctuids above 100 m AGL.

Radar has been used to detect and monitor the vertical distribution and flight characteristics of organisms the size of *H. zea* above 100 m AGL (Table 1). The radars use a parabolic dish antenna to transmit a pencil-shaped beam of energy that is reflected back from airborne noctuids and other flying organisms. By definition, radar systems are capable of determining the range (distance) of detected organisms. By determining the radar reflectivity of airborne organisms, a maximum detection range can be assigned. Several X-band radars reported here can detect individual *H. zea* at a maximum detection range of \( \sim 2.4 \) km. Echo intensity from all organisms in the pulse volume of the radar beam is measured to determine the aerial density of the organisms at a specific range (and associated altitude).

Four different operational modes of X-band (3.2 cm wavelength) radar have been applied for detection of individual *H. zea*-size organisms in the lowest 1000–1500 m AGL. One of the most common entomological radars operates in a circular scanning mode (Wolf et al. 1986). In the case of scanning radars, a pair of range rings defines a range interval annulus from which to integrate around the radar or within selected sectors (e.g., to monitor a migration flight that is localized in a portion of the radar scanning area). Vertical radars represent a second operational mode that directs the radar beam toward zenith and operates continuously (Beerwinkle et al. 1994, 1995). By rotating (and nutating) the antenna feed and consequently the radar beam, vertical radars can acquire characteristics (length, width, displacement speed, displacement direction, and mass) of organisms when single organisms are present within a selected pulse volume (Smith et al. 1993; Harman and Drake 2004). Also, continuous monitoring of a fixed beam orientation permits the collection of wing beat frequencies, which can further characterize flying organisms. A third operational mode is achieved by mounting vertical radar in an aircraft to monitor vertical profiles of noctuids beneath the aircraft (Hobbs and Wolf 1996). A fourth implementation of X-band radar is tracking radar, which actively adjusts the orientation of its antenna to maintain maximum detected radar reflectivity from a single organism. The radar can effectively track a noctuid moth when densities are low, but the track will be lost if there are so many insect (or other) targets that most pulse volumes return a comparably strong (or stronger) echo.

The U.S. national network of WSR-88D Doppler radars also has been deployed for monitoring weather conditions (Crum and Alberty 1993), but
Doppler radar data have also been used to assess noctuid migration. The WSR-88D radars operate at 10 cm wavelength and are more powerful than X-band radars, having a capability to detect wind velocities to a maximum range of 200 km and precipitation to a maximum range of 400 km. However, WSR-88D radars operate with the same scanning principle as the scanning X-band radars. The range interval volume (RIV) of the WSR-88D radar is \( \sim 1 \text{ km}^3 \) at a range of 100 km. Bulk radar reflectivity represents the integration of the transmitted radar energy reflected back to the radar by each noctuid and other organisms in the relatively expansive RIV. The WSR-88D radar also measures radial velocity of targets, which can be used carefully to calculate the collective ground speed and displacement direction of migrating noctuids. If wind data are available concurrently, the collective flight speed and heading of migrating noctuids can also be determined. Also, the radar beam centerline is above 1000 m AGL at elevation angles greater than, or equal to, 0.5° and ranges beyond 100 km. The large RIV of the WSR-88D radar can create a problem with the lack of uniform radar beam-filling by \( H. \text{zea} \) and other noctuids horizontally across the landscape and vertically in the atmosphere. In other words, the RIV of the radar beam may include more of the atmosphere in which noctuids are absent at the time of measurement, thus decreasing the concentration of targets and the bulk reflectivity within the RIV.

A nocturnal aerocological boundary layer is defined here to underscore the need for a biologically-based classification of the depth of the atmosphere in which organisms disperse. In atmospheric science, the atmospheric boundary layer (ABL) is defined as the layer of the atmosphere where surface friction influences atmospheric flow. The depth of the nocturnal ABL often decreases due to radiational cooling and formation of a low-level temperature inversion that inhibits the influence of frictional effects above the inversion. However, insects, birds, bats, and flightless organisms including spiders, pollen, and spores often are present at altitudes far above the ABL. Although the majority of direct biological sampling at night is predominantly contained within the ABL, the presence of dispersed organisms above the nocturnal ABL is acknowledged based on radar observations and limited physical sampling. Therefore, the depth of the nocturnal aerocological boundary layer is not quantifiable strictly based on atmospheric factors, but also must account for the presence, viability, and behavior of the airborne organisms.

Atmospheric variables within the nocturnal aerocological boundary layer have been measured traditionally using pilot balloons and radiosondes. However, radar wind profilers and WSR-88D radars can provide vertical profiles of wind speed and wind direction, and satellite radiometers can provide vertical profiles of air temperature.

Climatological research of the nocturnal ABL has detected a low-level wind jet in the Central US (Bonner 1968; Bonner and Pagel 1970). The low-level wind jet extends from southern Texas through Oklahoma to upper Midwestern US. The altitude of the low-level wind jet is \( \sim 600 \text{ m AGL} \). The low-level wind jet accelerates during the night, and may reach a maximum of 28 m s\(^{-1}\). The geographic location, altitude, timing, and speed of the low-level wind jet combine to create a favorable corridor for the nocturnal dispersal of noctuids and other organisms (Johnson 1995; Isard and Gage 2001). Although the low-level wind jet does not occur every night, it is a frequent feature within the nocturnal aerocological boundary layer. The atmosphere above and below a low-level wind jet, or in the absence of a wind jet, are part of the aerocological boundary layer if atmospheric conditions including minimum air temperature, relative humidity, barometric pressure, etc. can support the viability and flight of airborne organisms.

**Migratory flight of noctuids**

Adult corn earworms initiate migratory flight no sooner than the night following emergence from pupae. The initiation of nightly migratory flight is largely confined to the period from 0.5 to 1.5 h after sunset. Night vision measurements of \( H. \text{zea} \) flight above a cotton field in the LRGV revealed estimated temporal patterns of airborne moth concentrations that approximated local entomological scanning radar estimates (Raulston et al. 1995). *Helicoverpa zea* ascend in a spiral flight pattern to at least 50 m AGL, where they begin to level out into oriented flight (Lingren et al. 1995). An ascent rate of 1 m s\(^{-1}\) has been measured for individual \( H. \text{zea} \) using night vision equipment (Lingren et al. 1995) and for collective ascent of large populations of \( H. \text{zea} \) using entomological radar (Wolf et al. 1994). The main ascent phase occurs during the first 20 min of flight. The ascent angle was found to average 45° in the lowest 50 m AGL and decrease to an average of 30° from 50 to 100 m AGL as measured using night-vision binoculars (Lingren et al. 1995).

High-altitude sampling of night-flying insects has resulted in rather limited collections of \( H. \text{zea} \) and other noctuids. Using 0.16 m\(^2\) nets towed by
fixed-wing aircraft, 21 H. zea were among 110 noctuid specimens captured in Texas at altitudes from 60 to 1768 m AGL; among the captured H. zea, the majority were males and all females were virgin (SD Pair, unpublished). A rotary-wing aircraft towed a 5 m² insect net and captured several noctuid species but no H. zea (Beerwinkle et al. 1989). A single H. zea was captured as high as 2347 m in the LRGV (WW Wolf, unpublished data cited in Lingren et al. 1995). Light traps mounted on a radio tower captured H. zea as high as 349 m AGL, and revealed seasonal patterns of migratory flight activity (Callahan et al. 1972).

Once airborne, migrating noctuids re-distribute vertically throughout the night. Radar sequences often reveal one or more layers of noctuids, which change in concentration and altitude during the night. The maximum concentration of noctuids within a 50–100 m atmospheric layer is on the order of $10^3$–$10^4$ per million cubic meters (Beerwinkle et al. 1994). When layers of noctuids were present in the LRGV during spring 1982, the noctuid layers were associated with an average wind speed that was 2.4 m s$^{-1}$ greater than that at the altitude of minimum noctuid concentration (Fig. 1). However, difference between wind speed at the altitudes of maximum and minimum noctuid concentration ranged from $-2$ to 10 m s$^{-1}$ which indicates that while noctuids exhibited a propensity to fly in strong wind there are times when layers of noctuids were associated with lower-speed wind. Also, noctuid layers were associated with more stable atmospheric conditions as indicated by an average Richardson number that was 0.64 greater than that at the altitude of minimum noctuid concentration (Fig. 2). The difference in Richardson number at the altitudes of maximum and minimum noctuid concentration ranged from $-2.5$ to 3.5 indicating that layers of noctuids occasionally occurred in unstable atmospheric layers.

The average flight speed of individual migrating noctuids is $\sim$4.5 m s$^{-1}$. Flight headings of individual adult corn earworm are frequently distributed about the downwind vector. Also, collective flight orientation, represented as a bisected annulus on the radar plan position indicator (PPI) display, reveals seasonal patterns of flight orientation that frequently exhibit substantial crosswind angles (Wolf et al. 1995). Various magnitudes of collective orientation have been observed as expressed by relative radar reflectivity. Influences of cloud cover on insect orientation have not been established for H. zea and other noctuids.

An aircraft with an airborne radar flew transects across southern Texas to monitor the nocturnal migration of H. zea. By analyzing radar measurements along the flight transects, Wolf et al. (1990) identified the physical dimensions and trajectory of a “cloud” of H. zea migrating from the LRGV of Texas. Using half-power distances from the peak radar reflectivity in the center of the moth “cloud”, the cloud dimensions were found to be comparable to the dimensions of the source area, 200,000 ha of irrigated corn in the LRGV. Successive radar transects of the moth “cloud” during a single night identified a 400-km migratory flight displacement in 7.8 h.

Atmospheric trajectories have been analyzed to identify nightly patterns of long-distance migration of H. zea during periods of mass emergence in source areas (Westbrook et al. 1995b). Historically, atmospheric trajectories have been calculated using wind profiles generated from a sparse array of radiosonde stations. However, mylar balloons (tetroons) were...
released at the time of local *H. zea* flight initiation and ballasted to drift as surrogate markers at the estimated altitude of maximum concentration of migrating *H. zea* (Westbrook et al. 1995a, 1997). Calculated atmospheric trajectories representing nightly *H. zea* migration in the spring 1994–1996 were validated (Fig. 3) through the capture of Citrus pollen-contaminated *H. zea* in a network of pheromone traps that extended as far as 660 km from the LRGV (Westbrook et al. 1998).

Clear-air reflectivity images recorded by WSR-88D radars have revealed patterns consistent with noctuid migrations. For example, an outbreak of beet armyworm (*Spodoptera exigua*) occurred in cotton in the LRGV in June 1995. The WSR-88D radar at Brownsville, Texas, detected a cluster of high radar reflectivity that originated from an area of known *S. exigua* infestation ~80 km northwest of Brownsville, and displaced downwind to the northwest (Fig. 4). Reflectivity in the suspected cluster of noctuids attained a maximum value of 16 dBz. The area of maximum reflectivity decreased as the cluster displaced farther from the Brownsville WSR-88D radar. The increasing RIV may largely explain the decreased area of maximum radar reflectivity with increasing range from the WSR-88D radar.

The duration of noctuid flight appears to be limited to the scotophase, the dark segment of a light-dark cycle. However, a portion of a migrating population of noctuids may terminate flight prematurely. Strong wind shifts, with or without associated precipitation and sub-optimal air temperature, may force migrating noctuids to abruptly terminate flight. *Helicoverpa zea* and other noctuids, however, may continue flight during the photophase, or the

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**Fig. 3** Atmospheric trajectory map and associated capture of *H. zea* in a network of pheromone traps in Texas on 1995 March 22. Solid dot symbols indicate trap locations and star symbols indicate trap locations where citrus pollen-contaminated *H. zea* were captured. The atmospheric wind trajectory is a 12 h nocturnal estimate of *H. zea* migration at 500 m AGL using wind velocity values from the National Weather Service network of upper-air stations.

**Fig. 4** Clear-air radar reflectivity images recorded by the 0.5° elevation scan of the WSR-88D Doppler weather radar at Brownsville, TX, on June 11, 1995 at: (A) 0300 UTC, (B) 0349 UTC, (C) 0429 UTC, and (D) 0518 UTC. The range rings are at 25 km intervals to a maximum range of 200 km from the WSR-88D radar. The displayed areas of orange and red (8 and 12 dBz reflectivity levels, respectively) at a range of 100–175 km northwest of the Brownsville WSR-88D radar are associated with a suspected migration of *S. exigua*. 
illuminated segment of a light-dark cycle, when flying over open bodies of water such as the Gulf of Mexico (Wolf et al. 1986).

Successive nocturnal flights appear likely based on capture of pollen-contaminated *H. zea* > 800 km from the nearest possible source areas (Lingren et al. 1993, 1994) or local emergence of moths several weeks earlier than predicted (Hartstack et al. 1982). Suces\-sive flights may increase access to available nectar resources for replenishing flight fuel and increasing range expansion.

**Consequences of migration**

Migratory flight of *H. zea* and several other noctuid species allows these pests to quickly disperse across a broad geographic range and opportunistically exploit available host plants. Using the HYSPLIT atmospheric dispersion model (Draxler and Rolph 2003; Rolph 2003) to estimate nightly migration of *H. zea* from corn-producing counties, estimates of northward migration of *H. zea* during the corn-growing season (Fig. 5) and southward (reverse) migration during the fall (Fig. 6) illustrate the suspected broad geographic extent and rapid displacement of *H. zea* migration. It has been assumed that *H. zea* and other moderately-strong fliers colonize new habitats more quickly than do their natural enemies, thus fostering rapid growth of pest populations. Additionally, migration increases gene flow and may lead to the spread of resistance by noctuid pests to insecticidal compounds in pesticides (Westbrook et al. 1990) and transgenic crops (Pietrantonio et al. 2007). Future development and implementation of entomological radars and entomological applications of WSR-88D radars may increase the knowledge of migratory flight behaviors and aid in monitoring or estimating migration events.

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