Interface Modeling for Predicting Atmospheric Transport of Biota

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1. Introduction

The influx of foreign organisms and the growing resistance of resident organisms to chemical controls are coming at a time of increasing world population and need for greater efficiency in food production in the face of changing world climate. Rapid transportation and increased world trade have introduced foreign pests into American agricultural areas. Pesticides are increasingly ineffective at controlling insects and may have harmful side effects. As insects adapt to existing practices of crop rotation on a field-to-field basis and extend their ranges in a changing climate, it may become necessary to implement mitigation agricultural strategies such as crop rotations over regions or perhaps across international boundaries.

There is therefore a need for more thorough understanding of the biology of airborne organisms and for improved prediction of the transport and dispersion of biota. Vast numbers of biota are airborne over America annually. They range from pathogens and pollens which drift passively once airborne, to insects for which flight behavior contribute to transport, to birds which can fly any direction regardless of winds but usually take advantage of favorable winds during migration. By far the largest numbers of airborne biota are of the passive kind.

This study focuses on methods to predict accurate migration pathways for flying insects. It is assumed that horizontal flight speeds are small relative to the wind. However the ability of flying insects to impact migration pathways is not negligible. Environmental factors influence the altitude of insect flight. Therefore these factors can have significant impact on migration pathways especially under conditions of strong directional wind shear as occurs frequently over the Mississippi flyway during spring.

Figure 1 shows five stages of the process of insect migration beginning with preconditioning and ending with colonization of new habitat. Predicting migratory pathways requires information on the second through the fourth stages - takeoff and ascent, horizontal transport, and descent and landing.

Developing accurate predictions of migratory pathways requires information from biologists and meteorologists. Biologists provide information on location of liftoff, when liftoff begins, how long liftoff lasts, and relative number density of insects as a function of time during liftoff. Biologists also provide data on the environmental dependency of horizontal flight speed, orientation, and vertical ascent rates. Finally, biologists provide data on factors that cause descent.

Meteorologists provide accurate high-resolution (temporal and spatial) weather data. Especially important for estimating migratory pathways are high-resolution temperature and wind data within the lowest 1500 m of the atmosphere. A model that links the biological and meteorological data and generate accurate predictions of migratory pathways are the subject of this paper.

2. Background

Many of the techniques developed prior to 1985 to diagnose and/or predict the transport of biota within the Mississippi Flyway and elsewhere were summarized by Scott and Achtemeier (1987). Most of these methods involved construction of back trajectories using layer-averaged winds through the depth of the atmosphere thought to contain the traveling insects. Scott and Achtemeier used detailed vertical resolution of upper air soundings to show that greater precision is possible when diagnosing and predicting migratory pathways if biologists know the elevations where the migrants are flying. Numerical weather models can generate weather data with much finer spatial and temporal resolution than that presented by Scott and Achtemeier. These models are increasingly more accurate and model output is becoming routinely available to biologists.

One important determinant of flight behavior is air temperature. Vertical ascent rates are, at least in part, functions of temperature. Flight altitudes are, at least in part, determined by the vertical temperature structure of the lower atmosphere. However, airborne insects may respond to a number of environmental stimuli. Achtemeier (1992) used Doppler radar to study anomalous flight behavior within a cloud of grasshoppers (*Melanoplus sanguinipes*) contained within a strong updraft. These data permitted several hypotheses for the apparent disturbed flight behavior such as reorientation and falling of insects upon reaching flight threshold temperature, response to rapid rates of change of temperature and pressure upon

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ascent in strong updrafts, turbulence, and clouds - either encounter with cloud droplets or darkness beneath deep cumulus clouds.

Environmental dependencies of biota discovered in the field or in the lab by biologists can be quantified and introduced into the data stream of weather prediction models. The results, hypothetically, should be capable of predicting insect transport and locations of deposition much more accurately than from constant level trajectories (Showers, et al., 1989, 1993) because the changing elevations during insect flight will be known with greater precision. Knowledge of transport elevations is especially critical to the success of model predictions when there exists extreme wind direction shear within the lower atmosphere such as was found over the lower Mississippi Flyway by Scott and Achtemeier (1987).

Blending biological data with meteorological data has been successful in the prediction of the transport and deposition of airborne microbes. The Lighthart and Kim (1989) physical model for the dispersion of droplets of water containing microbes is an example. The Main, et. al, (1998) operational model for forecasting long-range dispersion of tobacco blue mold describes the viability of the pathogen as a function of duration of exposure to direct sunlight while airborne. Then this information is linked through a numerical trajectory model to predict the location and threat of pathogen spread.

3. How blending biological data with weather data can improve predictions of migratory transport - an analytical example

The analytical example assumes a simple linear dependency between temperature and insect rise rate in flight. Suppose an insect orients to fly with a horizontal velocity, u, and with a rise rate, w, as is shown in Figure 1. Let the rise rate be measured within a laboratory apparatus (Isard and Irwin, 1996) and relate lift to air temperature. Thus, as shown by the connected vectors in Figure 2, rise rate decreases as temperature decreases with altitude and the trajectory levels off to horizontal flight at an altitude where the insect maintains just enough lift to offset its body weight.

Let the hypothetical insects be a population of noctuid moths that take off at sunset, fly throughout the night, and land at sunrise. Suppose laboratory measurements establish a relationship between rise rate and temperature for a single individual as shown in Figure 3. There exists some temperature, T_0, defined as the flight threshold temperature, for which the insect is able to maintain lift just sufficient to offset body weight and for which the insect is just able to maintain level flight. Figure 4 shows the relationship for an ensemble of insects. Strong (weak) fliers are defined as those individuals that have the colder (warmer) threshold temperatures. Alternatively, strong (weak) fliers are defined as those individuals that have the fastest (slowest) rise rates for a given temperature. The rise rate/temperature relationship for the k_{th} insect is

$$w_k = c(T - T_0) + r_k \Delta w; \quad (1)$$

Let T_0 = 21.5C and c = 0.1555, and Δw=0.5 ms^{-1} so that the rise rate is 0.7 ms^{-1} ± 0.25 ms^{-1} at T=26C. The multiplier, $-0.5<r_k<0.5$ is a random number. Furthermore, assume that rise rates within the range Δw have an equal probability of occurrence.

Biological information is combined with meteorological data to produce accurate migratory pathways through a "Monte Carlo" particle generation model designed to track large numbers of "particles" that represent individual insects. Each particle is assigned a rise rate as a random number within the velocity range, Δw. Each particle lifts off from the ground and ascends according to the temperature-dependent rise rate given in Equation 1. The model keeps track of the horizontal and vertical locations of all particles and calculates locations of deposition when particles descend to the ground. The model also builds vertical profiles of particle density thereby producing time-dependent patterns of insect location throughout the atmosphere.

For this analytical study, let the biological information be given by the ensemble rise rate information from Equation 1 and figure 4, the start time for insect liftoff (1800 LST), the duration of liftoff (10 min), and the location(s) of liftoff. Insects will descend at sunrise. Let the meteorological conditions be those shown in Figure 5. Two schematic temperature profiles, one created for 2000 LST in the evening and the other created for 0600 LST the following morning, describe the key meteorological conditions for the period of the simulation. Weather conditions prior to 2000 LST are constant and are described by the evening profile (circles). The evening profile represents the state of the lowest 1500 m of the atmosphere just two hours after sunset. Boundary layer stabilization has commenced; weak reversals of the sign of the lapse rate of temperature (inversions) appear just above ground and near 500 m. The strength of the upper inversion is approximately 1C.

The morning profile (x's) represents a cooled, predawn airmass into which the insects have been transported. During the period 2000 LST to 0600 LST, the atmosphere above 500 m cooled 2C. Greater rates of cooling below 500 m changed the temperature structure to that shown for 0600 LST.

The hypothetical insect lift-off begins at 1800 LST and lasts for 10 min. The particle model launches 24 particles at 20 sec intervals for a total of 720 particles. The particle rise rate is randomized subject to Equation 1. Figure 6a shows the distribution of particles immediately after lift-off. Since this is a hypothetical case, absolute numerical values are not assigned to the graph of number density. Relative magnitudes can be inferred by the extension of darkened areas to the right of the baseline. The sloped line at the far right side of the figure is the 2000 LST vertical temperature profile.

Although the particles were released at the

same rate over 10 min, velocity sorting skews the distribution as particles with faster rise rates (the strong fliers) rise above of the larger body of particles. The same pattern of particles appears near 500 m, the altitude of the temperature lapse rate inversion, by 1825 LST (Figure 6b). The absence of change in the overall shape of the cloud is suggestive that the small variations in temperature between 500 m and 700 m did not impact particle rise rates - at least on the scale of the particle cloud.

The situation changed by 1840 LST (Figure 6c). A relative minimum in the particle number density pattern is present near the top of the inversion at 700 m. Elsewhere, the fine scale maxima in the vertical profile of the number density distribution are produced by the randomization procedure and no significance regarding particle "flight behavior."

The particle cloud evolved into two separate layers shortly after 1900 LST. Figure 6d shows the two separate layers at the completion of the ascent stage at 2000 LST. The weak fliers leveled off at threshold temperatures below the inversion at 500m. Meanwhile the average to strong fliers ascended to threshold temperature levels 200 m to 400 m above the inversion.

Between 2000 LST and 0600 LST, the model atmosphere cools 2C. When temperatures fall below threshold temperatures, the hypothetical insects are no longer able to maintain level flight. Thus the cool down forced particles to descend to altitudes where warmer temperatures were at the threshold temperature or until the particles fell to the ground. Figure 7a shows that both layers of particles descended approximately 100 m . The lapse rate of temperature below 500 m became more isothermal. Continued cooling of the nocturnal boundary layer reversed the lapse rate (see the 0600 LST sounding in Figure 5). When that happened, particles descended into colder layers and were deposited at the ground. The weak fliers fell out before 0600 LST (Figure 7b). Strong fliers descended to the top of the inversion. Average fliers descended below the inversion and were falling out.

4. Discussion

As regards predicting transport and deposition of airborne biota, we may make several observations about the results from the simple linear model of rise rate versus temperature. First, the altitudes of particle flight were time-dependent. Strong fliers leveled out at flight threshold altitudes well above the altitude of maximum temperature located at the top of the nocturnal inversion. Riley, et al., (1991) in their study of long distance migration of the brown planthopper [*Nilaparvata lugens* (Stal)] found the migration height above the top of the surface temperature inversion meaning the migrants did not fly at the height of the warmest air. *N lugens* continued climbing until they reached a height at which air temperatures approached those too low for flight. Then the insects accumulated below this flight ceiling.

Simulated flight levels lowered as the atmosphere cooled during the night. Riley, et al. reported that researchers in central and south China caught *N lugens* between altitudes of 500 and 1000 m at the end of September and in October but in November most were caught lower down between 200 and 800 m. They ascribe these differences to seasonal variations in the average height at which flight ceiling temperatures occur. Thus, though the lowering of the elevation of the flight levels was part of a seasonal cool down, the connection between flight level and threshold temperature is the same as was found for this study.

Wolf, et al. (1990) observed a cloud of *Heliothis zea* (Boddie) in northward migration over Texas for distances up to 421 km from the source region during June 1989. From 2145 LST to 0415 LST, the cloud of maximum insect concentrations descended from approximately 600 m to 400 m. Vertical temperature profiles were not presented, however at least some of the reduced flight ceilings can be explained by insects transported northward into a cooler regime and by nocturnal cooling.

This simple model simulates some time-dependency of insect flight ceilings not unlike those observed by other investigators. However, the most important outcome of this simulation is that no single-level trajectory will suffice to give accurate migratory pathways for night-flying insects, particularly in the presence of significant directional wind shear.

Second, simple temperature stratifications produced complex particle layering. Many observers (Wolf, et al.,1990; Drake, et al., 1981; Riley and Reynolds, 1983; McLaughlin, 1994; and others) have documented insect layering by radar. Collocated temperature profiles showing no stability structures explained the single insect layer found at 2 km (10C) over New Mexico by McLaughlin. Riley, et al., (1991) suggested insects climb to the level of the flight threshold temperature and level off there.

In the example given in this paper, a 1C inversion of the temperature lapse rate split the particle cloud into weak fliers and strong fliers. More complex temperature profiles containing fine scale stability structures (not necessarily inversions) could greatly complicate vertical distributions of particles beyond those shown in Figures 6 and 7. Furthermore, the results are for a single "species". Add in populations of other "species" with rise rate/temperature relationships unique to each and the resulting vertical distribution of particles becomes exceedingly complex.

This study did not include wind speed and direction. If the winds were from the southwest and were constant through the levels of insect flight, then the particle deposition "footprint" might look like that shown in Figure 8. Weak fliers fall out as a separate group. Then strong fliers precipitate out beginning with the weakest fliers of that group. Finally the remaining strong fliers descend at sunrise. In the event of strong wind speed and direction shear, the "footprint" may look much different from that shown in Figure 8.

Additionally, the size and shape of the deposition footprint is determined by the area and duration of insect lift-off from the source region and transport and dispersion within divergent windfields.

McCorcle and Fast (1989) developed a "concentration index" for modeling the distribution of black cutworm moths [*agrotis ipsilon* (Hufnagel)] assumed to be migrating from Texas into the corn belt on 500 m winds. Their initial liftoff area comprised roughly three fifths of Texas. After two days, the area enclosing non-zero concentration index extended from Louisiana to Minnesota and from Texas to Indiana.

The frequent occurrence of layering of insects during long-range flight led Drake and Rochester (1994) to posit that it might represent an adaptation - a behavior that might increase the probability of migrants reaching a destination where conditions are favorable to them. In addition, layering and/or orientation might represent an adaptation that keeps insects from being dispersed widely during transit within a shearing wind field with the result that insect populations upon deposition are sufficiently concentrated to be reproductively viable. The tendency for insects to fly in layers near the top of the nocturnal inversion just above the low level jet (Bonner, 1968) (an optimal elevation if long-range transport is the objective) has been well documented (Wallin and Loonan, 1971; Wolf, et al., 1986; Beerwinkle, et al., 1991; and many others). That insects have been oriented in specific directions during long-range transport also is well-known (Schaefer, 1976; Mueller and Larkin, 1985; Achtemeier, 1992; and many others).

Do insects participate in their transport so that layering and orientation influence the outcome in some advantageous way? Continued studies in the behavior of insects in various environmental conditions can help answer this question. Unless insect behavior observed in the laboratory gives direct evidence of active migration strategies, the biology of in-transit insect flight will have to be deduced from the difference between observed and modeled flight behavior. Remote observation instruments (Moore, et al., 1986; Mueller and Larkin, 1985; Riley, 1992; Achtemeier, 1992; and others) are capable of identifying flying insects by physiological features such as size, shape, orientation of flight, and wing-beat frequencies. Numbers of insects in flight and flight levels are also measured. In the event of the establishment of an aerobiological network of instruments, insect cloud dimensions and time variations in flight elevations will also be observed.

Complementing these observations will be the meteorological models. Meteorological models can be refined with upper air observations to increase the vertical resolution of temperature profiles. Should observations differ from model predictions, explanations will have to be sought beginning first with additional meteorological complications. Using FM-CW radar, McLaughlin (1994) observed insects flying along inversion layers, Kelvin-Helmholtz induced instability waves, gravity waves, and gust fronts. Vertical motions associated with these phenomena can displace insects locally. If models such as rise rate/temperature relationships fail to explain discrepancies between model predictions and observations, then the models may need to incorporate these higher-order meteorological phenomena. Once meteorological explanations for the discrepancies have been exhausted, then biological explanations involving migration strategies may be framed and subsequently verified in the laboratory.

Connecting the biology of airborne insects with meteorology for all stages of the migratory process will increase the accuracy of predictions of migratory pathways. There is economic promise in increased accuracy of forecasts of insect transport and dispersal. In addition, the prospect that insects might participate in the long-range phase of their migration is of particular interest to scientists seeking to understand insect response to environmental stimuli.

5. References

References available on request.

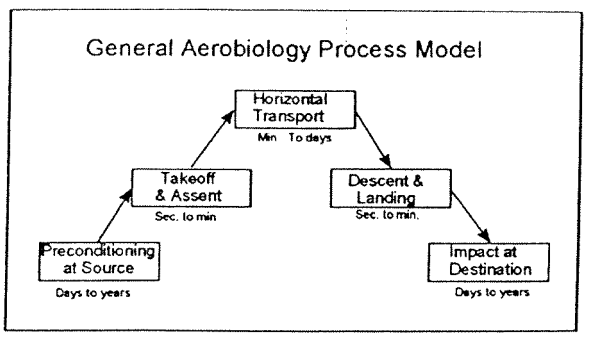

Figure1. Schematic showing five general stages culminating in insect migration.

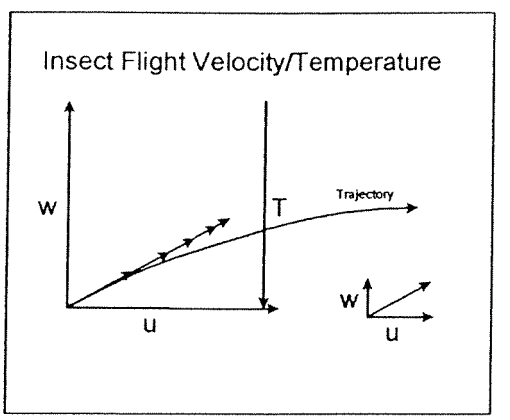

Figure 2. Schematic of the relationship between rise rate and temperature for an insect in the ascent stage of migration.

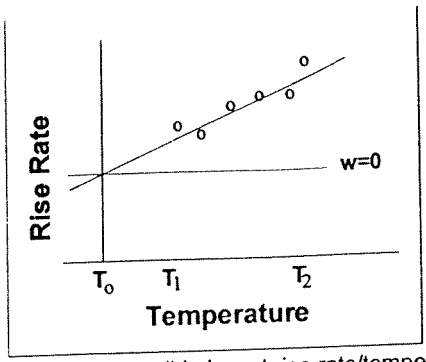

Figure 3. A possible insect rise rate/temperature relationship.

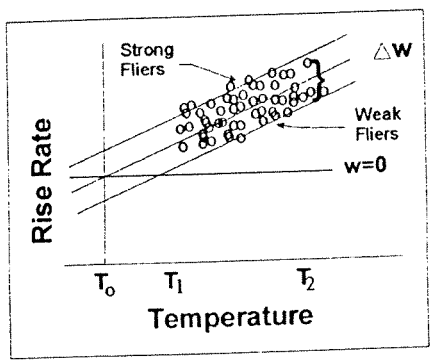

Figure 4. Same as Figure 3 but for an ensemble of insects.

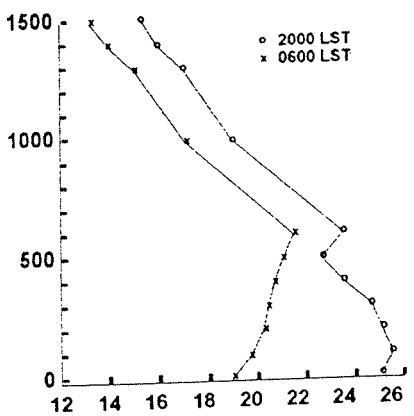

Figure 5. Schematic temperature sounding along insect migration pathway near sunset (circles) and near dawn (x's).

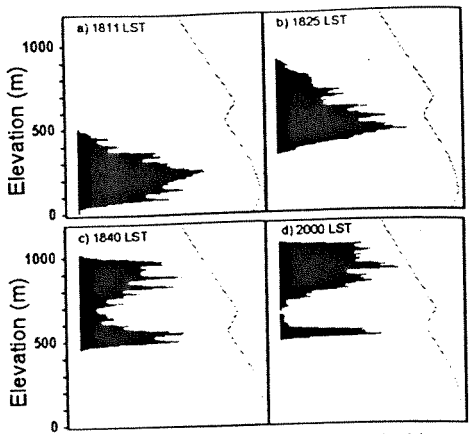

Figure 6. Vertical distribution of modeled insects during the ascent phase.

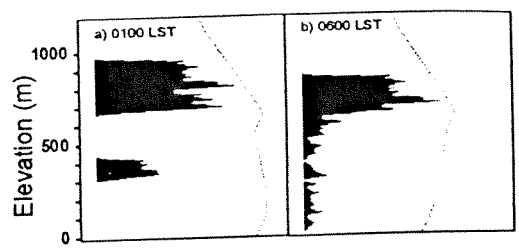

Figure 7. Vertical distribution of modeled insects during the transport phase.

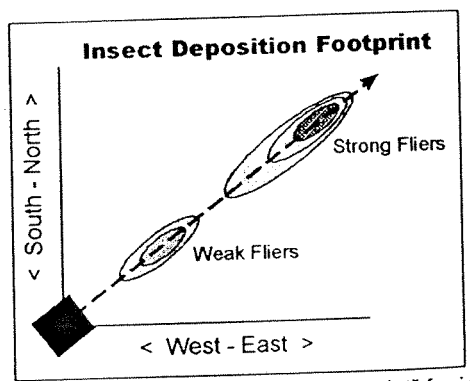

Figure 8. Schematic deposition "footprint" for insect flight behavior described by Equation 1 and matched with weather conditions described by Figure 5. Southwest winds assumed constant with height and invariant in time.