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4.3 A FRAMEWORK FOR STANDARDIZING FLIGHT CHARACTERISTICS FOR SEPARATING BIOLOGY FROM METEOROLOGY IN LONG-RANGE INSECT TRANSPORT

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1. INTRODUCTION

Once airborne during long-range transport, to what extent is the final destination determined by the biota? It is well known that a biological mechanism initiates flight and another biological mechanism terminates flight. Therefore, efforts to answer the above question should be focused on en route insect behavior.

In the transport of pollens, seeds, spores, etc., the biological component is usually restricted to the aerodynamic design of the substance being transported. The mechanism of transport is meteorological and therefore considered passive. The transport of insects, however, is another matter. Insects can play an active role in their transport.

The tendency for insects to fly in layers at or near the elevation of the low level jet (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). What biological, meteorological, or combinations thereof place insects in close proximity to the elevation of the low-level jet?

The tendency for insects to be oriented in specific directions during long-range transport also is well-known (Schaefer, 1976; Mueller and Larkin, 1985; Achtemeier, 1992; and many others). Is orientation part of a strategy to gain access to downwind food sources or is orientation just a fortuitous "adjustment" of insects in group flight?

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. Knowledge of this behavior might be of use to pest forecasters.

There is economic promise in increased accuracy of forecasts of insect transport and dispersal. However, 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.

A strategy is proposed to isolate biology from meteorology of long-range insect transport. The scheme has four parts: 1) laboratory observations of insect flight, 2) an insect flight-level weather model, 3) observations of the thermal stratification of the lower troposphere, and 4) observations of insects in flight. Measured temperature/rise rate relationships can be entered into a time-dependent meteorological model. The model can simulate flight elevations as functions of vertical temperature stratification for an ensemble of insects. Model results can be compared with observations of insects in flight. Similarities between observed and modeled flight levels should be attributed to temperature/rise rate dependency. Differences between observed and modeled flight levels should be ascribable to higher-order meteorological phenomena and to biological factors. Identifying and eliminating other weather factors should yield the biological component of long-range insect transport - if any.

2. INSECT FLIGHT MODELING STRATEGY

Laboratory measurements of insect flight

Laboratory measurements of insect flight draw on knowledge that flying insects are cold-blooded animals, that is, body temperature is controlled by the temperature of the air through which the insect flies. Wing-beat frequency, hence lift, is directly related to air temperature.

Isard and Irwin (1996) constructed a flight chamber to measure aphid rise rates for different wind and stability conditions. Suppose a flight chamber similar to theirs is available for routine measurements of rise rates as functions of temperature. Suppose measurements of rise rates for a hypothetical insect are obtained for temperatures ranging from T_1 to T_2 as shown in Figure 1. If the relationship is linear, a regression line fit to the data may be extrapolated to find an air temperature for which insects are just able to maintain level flight.

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Now suppose that rise rate measurements are taken for an ensemble of insects as shown in Figure 2. For simplicity, assume the same linear rise rate/temperature relationship for all insects. The functional relationships thus differ only by a constant. Their regressions lines intersect w=0 at different

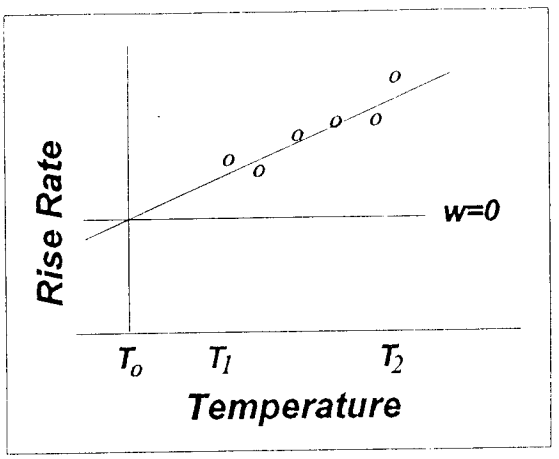

Figure 1. A possible insect rise rate and temperature relationship.

temperatures. If T(w=0) is warm, the insects are considered weak fliers; if T(w=0) is cold, the insects are considered strong fliers.

A flight simulation weather model

Simple laboratory-measured rise rates as functions of air temperature for an ensemble of insects are all that is required to model how temperature stratification influences insect flight level. Each insect has its own equation for rise rate as a function of temperature. A rise rate equation based on Figure 2 for the kth insect is,

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

where Δw is the range of vertical velocities found between weak and strong fliers and $-0.5 \le r_k \le 0.5$ is a random number assigned for each insect by the model.

The meteorological model uses these equations to calculate the elevation of each insect within changing vertical temperature stratifications. The model carries simple parameterizations for thermal instability and mechanical turbulence. Both forcings die off rapidly after sunset as the planetary boundary layer cools off.

Temperature-dependent insect flight levels are modeled as follows:

1) An ensemble of insects is assigned assent velocities according to the distribution shown in Fig. 2. The constants in Eq. 1 are c=0.14 m/sec/°C, T_0=21.5C, and Δw=0.5 m/sec. The range of rise rates between weak fliers and strong fliers is 0.3 - 0.8 m/sec at 25.5C, the maximum temperature found in the evening sounding

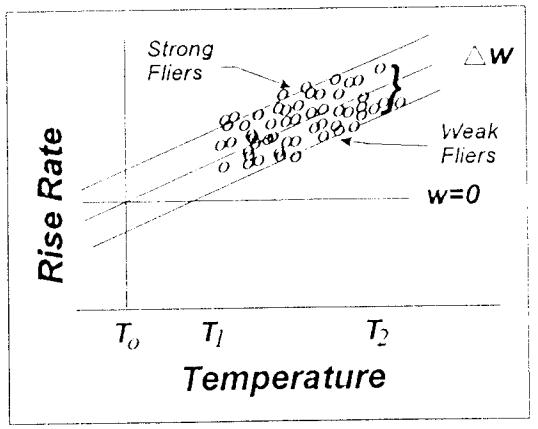

Figure 2. Hypothetical functional relationship between rise rate and temperature for an ensemble of insects.

(see Fig. 3).

2) Each insect starts from the ground and lifts off according to its temperature-dependent vertical velocity.

3) The model steps at 20 sec intervals and keeps track of the (x, z) locations of all insects. The results are updated graphically at each time step.

4) The vertical temperature structure is held constant from 1800 LST (sunset) til 2000 LST (Fig. 3) then is decreased linearly from 2000 LST to 0600 LST.

Meteorological Measurements

A meteorological model of the evolution of the vertical temperature structure in the lowest 1 km can range from the complexity of a radiation budget model to the simplicity of linear interpolation between a series of temperature soundings of the lower 1-2 km of the atmosphere. This model uses linear interpolation between soundings to approximate the nocturnal evolution of the temperature stratification.

Many studies of long-range insect transport have included collecting detailed measurements of the thermal structures of the atmosphere as part of the project design (Isard, et al., 1994; Wolf, et al., 1986, and others). The meteorological model is set up under the assumption that several temperature soundings spanning parts of the migration period are available.

Figure 3 shows two schematic temperature soundings used for the meteorological part of simulating insect flight levels. The initial sounding (circles) represents the state of the lowest 1500m of the atmosphere just several hours after sunset. Boundary layer stabilization has commenced; weak inversions appear just above ground and near 500m.

The strength of the upper inversion is approximately 1C. The second schematic sounding (x's) represents a cooled, predawn airmass into which the insects have been transported. Temperatures above 500m are 2C cooler. Below 500m, the sounding represents the cooled predawn surface layer.

Observations of insects in flight

The use of radar to observe the movement and behavior of migrating insects is a well-established practice in aerobiology. (For a partial list of references, see Drake and Rochester (1994)). Radar observations of

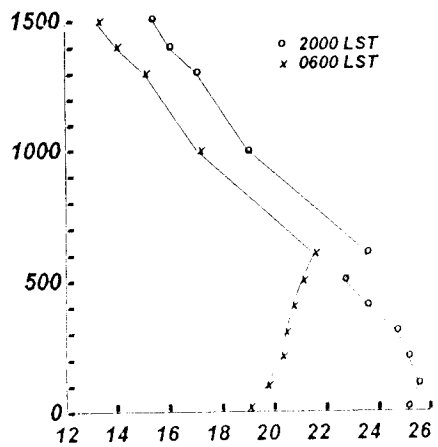

Figure 3. Schematic temperature soundings along insect migration route, near sunset (circles), near dawn (x's).

insects in flight are critical to the success of an effort to isolate the biological component of long-range transport. They provide ground truth against which model results are compared.

3. RESULTS

A burst of approximately 1000 insects lifts off at 1800 LST for a period of only 10 minutes. Fig. 4 shows the evolution of the initial cloud of insects into complex layers during the course of the night. Fig. 4a shows the initial burst of insects 11 minutes after lift-off. Since this is a hypothetical case, absolute numerical values are not assigned to the graph of number density. The sloped line at the far right side of the figure is the 2000 LST vertical temperature profile (Fig.3).

After 25 minutes, the insect cloud has lifted through the inversion at approximately 600 m without apparent response to the small variations in stability there (Fig.4b).

By 1840 LST (Fig.4c), a complex of layers has appeared. There are found two major layers, one located near the base of the inversion at 500 m, and the other located above the inversion at 800-1000 m. By 2000 LST, 2 hours after initial lift-off (Fig. 4d), the insects have consolidated into the two major layers.

Figure 4d represents the completion of the ascent stage; the layering of insects would not change from that of Figure 4d if the temperature structure remained unchanged. The weak fliers have become trapped below the inversion while the strong fliers have ascended to 200-400 m above the inversion.

The weather model cools the atmosphere linearly from the sounding of 2000 LST to that of 0600 LST. As the threshold temperature needed to maintain level flight has lowered in altitude, so have the insect layers. By 0100 LST, 7 hours after lift-off (Fig. 5a), the 300 m deep upper layer has descended to the top of the inversion. This is the level where the nocturnal jet maximum typically occurs. The weak fliers have descended to about 300-400 m above ground.

The weak fliers have fallen out by 0600 LST (Fig. 5b). There remains a single layer at and just above the top of the nocturnal inversion. The weakest of these fliers are precipitating out.

4. DISCUSSION

If rise rates as a function of air temperature are known for an ensemble of insects, they may be input into a simple weather model designed to simulate the role air temperature plays in the elevation and layering of insects in flight. This model has reproduced rather well many of the insect layers observed with temperature inversions and the low-level jet. These results suggest that the modeling approach proposed in this paper offers a potentially powerful tool for separating biology from meteorology during long-range insect transport and improving on forecasts of insect dispersion.

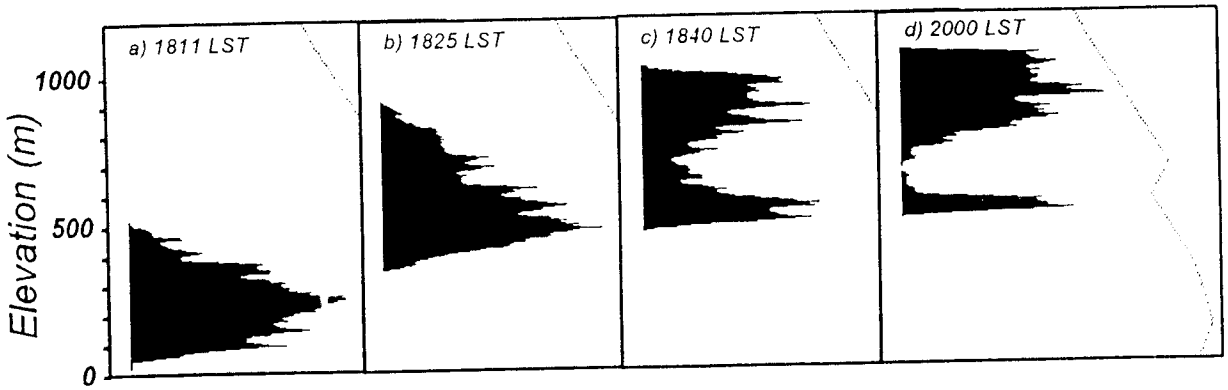

Figure 4. Vertical distribution of modeled insects during ascent phase.

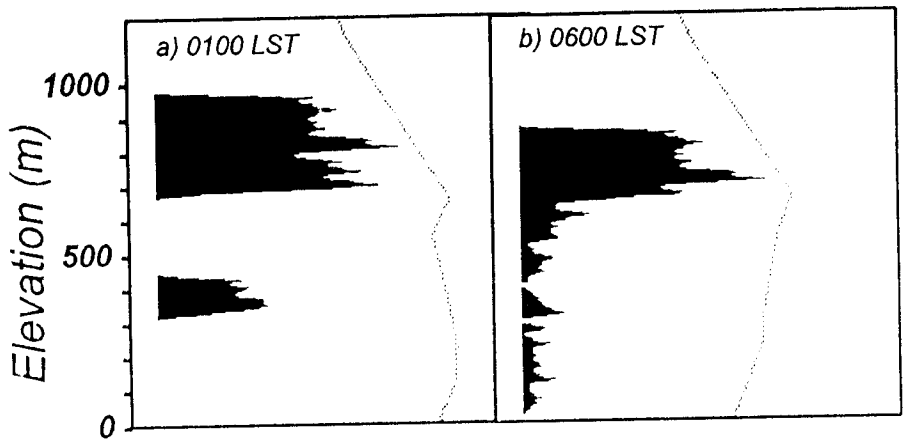

Figure 5. Distribution of modeled insects during transport phase.

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