

# A Simple Numerical Model of the Flight Behavior of Small Insects in the Atmospheric Convective Boundary Layer

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**ABSTRACT** We have combined aircraft and airborne Doppler radar observations to show that microinsects in the atmospheric convective boundary layer (CBL) are concentrated in rather well-defined plumes, that these plumes are generally found in thermals of rising air, and that the insects in those plumes oppose the updrafts at a rate that increases as the updrafts become stronger. In this paper, a simple numerical simulation of the airflow field and insect concentration in the CBL is developed. The model shows a consistency of the observed insect flight behavior with the presence of well-defined insect plumes in the otherwise well-mixed CBL and with the tendency of insects to cluster in updrafts. The model also explains the growth of insect plumes in the morning hours and their disappearance in the late afternoon. Other studies have proposed that the response of insects to being lofted high into the CBL is controlled by air temperature. Our simulation shows that a temperature-sensitive response alone does not yield well-defined plumes in regions of rising air currents. The observed flight strategy may be counterintuitive, but we suggest that it has a clear adaptive advantage.

**KEY WORDS** insect flight, atmospheric boundary layer, numerical simulation

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THIS STUDY FOCUSES ON the flight behavior of insects, primarily microinsects, in the atmospheric convective boundary layer (CBL). The CBL is the lowest part of the troposphere; it is roughly 1 km deep and is often capped by a stable layer or inversion (e.g., Stull 1988). It is not to be confused with the atmospheric surface layer (or insect boundary layer), which is only  $\approx 10$  m deep (e.g., Johnson 1969). The CBL has a clear diurnal cycle; it is absent at night and grows as a result of surface heat fluxes during the day. These fluxes are carried up from the surface layer in coherent eddies or thermals. Because these thermals are buoyant, strong vertical air currents may occur in the CBL, making the CBL a very turbulent environment.

Geerts and Miao (2005) used airborne Doppler radar and aircraft data collected in late spring of 2002 in the central Great Plains of North America to study microinsect flight behavior in the CBL. Their observations showed that insects in the CBL are concentrated in rather well-defined plumes (referred to as insect plumes), that the air generally rises in those plumes (i.e., that insects are found primarily in thermals), and that the insects in those plumes oppose the updrafts at a rate that increases as the updrafts become stronger. The first of these findings has long been established (e.g., Konrad 1970, Schaefer 1976, Reid et al. 1979, Gossard 1990). The second has been speculated (e.g., Drake 1982, Pedgley et al. 1982, Drake and Farrow 1989, Wilson et al. 1994, Russell and Wilson

1997) but never directly observed. The third finding is new. That finding implies that, on average, insects tend to subside in the CBL. This observation is not only counterintuitive (how then can insects persist in the CBL?), but it also seems incongruous with a body of aerobiological research that has focused on the question of how weakly flying insects manage to rise into the CBL, which is essential for them to travel the large horizontal distances that they have observed to travel (e.g., Johnson 1969, Isard and Gage 2001).

A number of entomologists, starting with Rainey (1955), have been using radars to study the dispersion and migration of insects (see <http://www.ph.adfa.edu.au/a-drake/trews/> for references). They have long recognized that the existence and persistence of radar "fine-lines," areas of sustained low-level air convergence, can be explained only by a biotic response (e.g., Schaefer 1976, Pedgley 1980, Drake 1982, Achtemeier 1991). This response has been assumed to be to lower temperatures at higher altitudes, because insects are poikilotherms. Schaefer (1976) suggested that in the upper parts of convective plumes, insects may slow down their wing beat or become entirely immobile because of the low temperatures. At some point, gravity exceeds the lift created or experienced by the insect, resulting in downward motion. Similarly, Achtemeier (1991) suggested that the insects oppose updrafts passively only where they encounter temperatures too low to maintain their wingbeat. He believed the radar scatterers in his study were mainly grasshoppers (*Melanoplus sanguinipes* F.). Symmons

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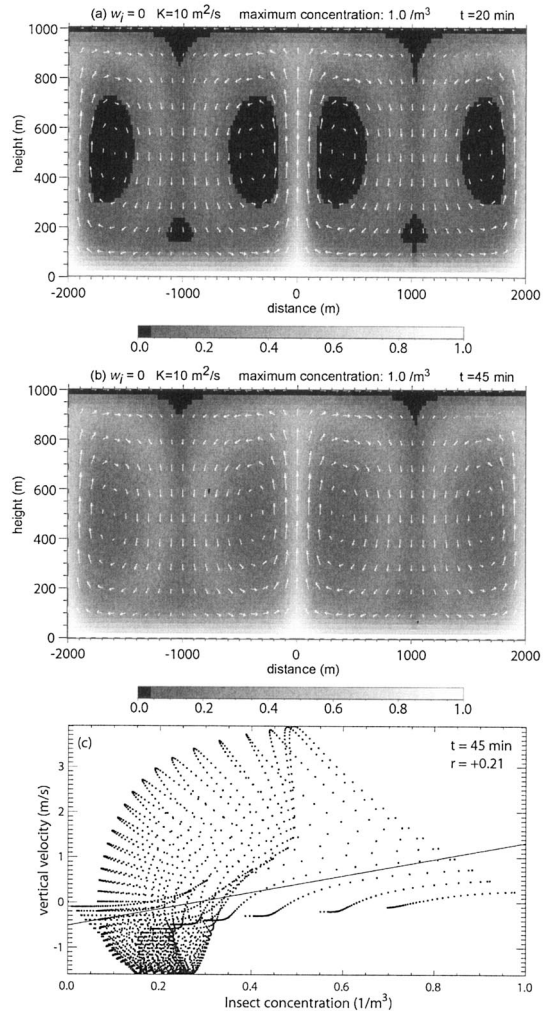
and Luard (1982) also assumed a temperature-dependent response in an idealized numerical simulation similar to the one presented in this study, but with wind shear, as a way to explain the development of high concentrations of *Chortoicetes terminifera* Walker (the Australian plague locust) in the vicinity of a frontal convergence zone. They assumed that as soon as the ambient air temperature falls below 20°C, *C. terminifera* descend at a speed of 0.4 m/s. Achtemeier (1998) made the assumption that, below some threshold temperature (21.5°C), the “subsidence rate” of strongly flying insects increases with decreasing temperature, whereas at higher air temperatures, the “rise rate” increases linearly with temperature. These models may apply to macroinsects that tend to travel at night.

This study casts doubt about whether the existence and persistence of plumes of microinsects in the CBL is controlled by air temperature.

We developed and used a simple numerical model to validate the consistency of the three observations by Geerts and Miao (2005). This model was used further to show that the observed echo plumes cannot be explained by microinsect subsidence when the temperature falls below some threshold. As further evidence that the scatterers are biotic and that they oppose updrafts, we also considered two other scenarios in which the scatterers do not respond to environmental changes: random movement and subsidence at a constant rate. Finally, the implications of the observed insect flight behavior, as presented in Geerts and Miao (2005) and corroborated here by means of a simple model, will be discussed.

### Materials and Methods

**Model Design.** The model represents an idealized, steady air circulation in which the insect concentration can change over time, to eventually come in equilibrium with the airflow. In reality, buoyant thermals in the CBL are rather transient, with a lifetime on the order of 1 h. For simplicity, the model airflow consists of a series of steady-state circulation cells as shown in Fig. 1. Each set of opposing cells is 2 km wide and 1 km deep, such that updrafts are periodic over a distance of 2 km. This is comparable with the observed CBL depth of  $\approx 1$  km and the observed plume spacing of 2–3 km (Table 1 in Geerts and Miao 2005). The flow field is computed on a regular grid with a grid spacing of 20 m in the horizontal and vertical dimensions. There is no mean horizontal wind or any wind shear (i.e., the gradient of the mean wind with height is zero). Furthermore, there is no horizontal or vertical airflow outside the circulation cells, i.e.,  $w = 0$  at the top and bottom, and  $u = 0$  at the lateral boundaries, where  $(u, w)$  is the two-dimensional airflow, as shown by vectors in Fig. 1. This vertical velocity field ( $w$ ) was contrived mathematically and tuned such that its distribution roughly matches the  $w_a$  distributions shown in Fig. 10 in Geerts and Miao (2005). In this flow, updrafts are stronger but more local than downdrafts, consistent with observations. In fact the maximum



**Fig. 1.** Insect concentrations in a hypothetical, steady airflow field.  $w_i$  is the insect response as described in the text. In this scenario, insects move randomly but are otherwise suspended in the air flow ( $w_i = 0$ ). The initial condition ( $t = 0$ ) assumes a concentration  $c = 1/m^3$  at the lower boundary and  $c = 0$  everywhere else. The image on top (a) applies for  $t = 20$  min and the middle one (b) for  $t = 45$  min. (c) Scatter plot of insect concentration versus vertical air motion for the insect distribution shown in b at  $t = 45$  min.

updraft of 3.9 m/s is 2.4 times larger than the maximum downdraft in the model circulation cells. The horizontal air flow ( $u$ ) was computed to obey air mass continuity in two dimensions, i.e., the mass of air is conserved locally. This condition implies that an updraft is rooted in convergent flow and topped by divergent flow. We examine microinsect dispersal in this steady flow field.

**Model Assumptions.** It is assumed that the insects do not travel horizontally, which implies that there is no flux of insects through the lateral boundaries. The model does not distinguish different insect types, sizes, or corresponding flight behaviors. For simplicity

the model only considers the concentration of insects, denoted as  $c$  (number/m<sup>3</sup>). The insect concentration in the air obeys the continuity equation as follows:

$$\frac{\partial c}{\partial t} = -u \frac{\partial c}{\partial x} - w \frac{\partial c}{\partial z} + \frac{\partial c w_i}{\partial z} + K \left( \frac{\partial^2 c}{\partial x^2} + \frac{\partial^2 c}{\partial z^2} \right) \quad [1]$$

where  $x$  and  $z$  are the horizontal and vertical distances respectively,  $t$  is time,  $(u, w)$  is the two-dimensional airflow, as defined above, and  $w_i$  is the insect response, as defined in Geerts and Miao (2005), i.e., the insect vertical motion relative to the air (m/s). By convention, the term  $w_i$  is positive if the insects move down relative to the air. The constant  $K$  is the eddy diffusivity (m<sup>2</sup>/s). The term on the left of Equation 1 is the local rate of change of insect concentration, and the four terms on the right are, from left to right, the horizontal advection, the vertical advection, the change in concentration because of insect vertical motion relative to the air, and the diffusion term. The latter represents both random (Brownian) insect motion and dispersal by the turbulent airflow fluctuations at a scale smaller than the coherent eddies shown in Fig. 1. These motions are assumed to be isotropic in horizontal and vertical directions. Isotropy applies rather well for turbulent eddies in the CBL, and microinsects may also move randomly in all directions. The eddy diffusivity  $K$  is a measure of the distance of random motion before the direction changes. For instance, a value of  $K = 1$  m<sup>2</sup>/s implies that insects (or turbulent air motion), traveling at a speed of 1 m/s, cover a distance of 1 m before changing direction.

All terms in Equation 1 are computed for each of the grid points of the regular grid. The flow field for each grid point is described above. First-order centered finite differences (Haltiner and Williams 1980) are used for the differential terms in Equation 1. In all cases, the initial state is assumed to be  $c = 0$  everywhere except at the ground ( $z = 0$ ), where  $c = 1/\text{m}^3$ . This condition is intended to supply a source of insects from the ground. It allows for upward diffusion and/or advection of insects into the CBL. The numerical code was written specifically for this application and was not based on any existing numerical model or software source.

**Model Scenarios.** We consider four scenarios. The first two scenarios assume that insects do not adjust their flight behavior to changing environmental conditions, whereas the last two assume that the insects respond to the cooler air as they are lofted in updrafts and to the updraft speed itself, respectively. The scenarios are (1) random microinsect motion only, where  $w_i = 0$  and  $K = 10$  m<sup>2</sup>/s; (2) the dead particle scenario, where at all grid points  $w_i = 0.45$  m/s (this is the average rate of insect subsidence revealed by a comparison of radar velocities with vertical air motion measured nearby; Geerts and Miao 2005); (3) the temperature threshold scenario, where  $w_i = 0.45$  m/s only above a level where the temperature falls below a threshold value; and (4) the updraft opposition scenario, where  $w_i = 0.42 + 0.49w$  (according to Equation 2 in Geerts and Miao 2005).

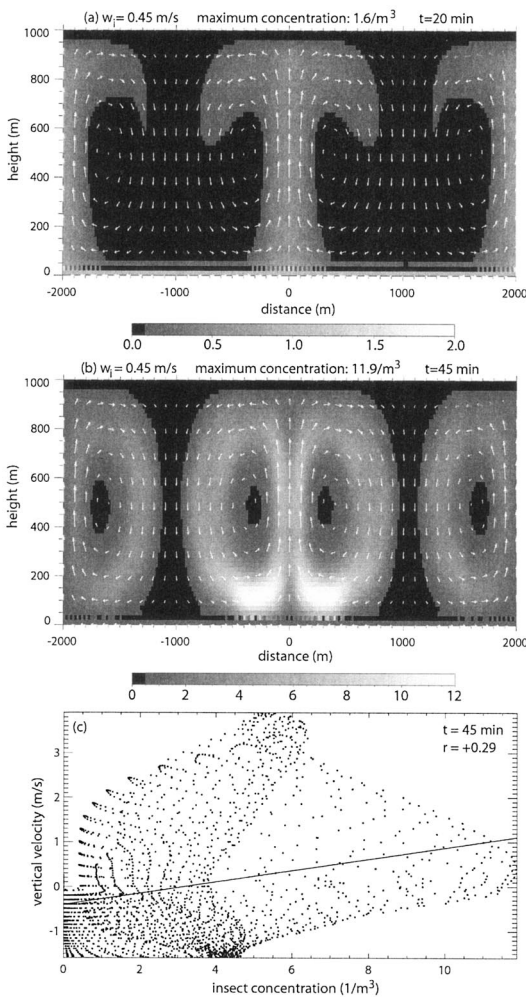
Because the fall speed and flight speed of microinsects is limited to 1–2 m/s (e.g., Wellington 1945, Johnson 1969, Thomas et al. 1977, Pedgley 1980), we impose a ceiling to this ability to oppose an updraft. That is,  $|W_{i, \max}| = 1.5$  m/s, as proposed by Geerts and Miao (2005). It should be noted that the temperature decrease with height is  $\approx 9.8^\circ\text{C}/\text{km}$  within the CBL; the variation from this lapse rate is small. Also, even though thermals tend to be buoyant (warmer than the surrounding air at the same level), the vertical temperature gradient is much larger than any horizontal temperature variation across thermals. Thus, for the temperature threshold scenario, a certain height can be assumed above which microinsects stop flying. If the insect flight threshold is  $20^\circ\text{C}$  and the CBL top measures  $17^\circ\text{C}$ , there is a 300-m zone in the upper CBL where the insects would fall or fly down. Here we assume the threshold height to be 700 m above ground level.

The airflow field is the same in all scenarios. In scenarios 2–4, it is assumed that  $K = 0$  to clearly separate the processes. Unfortunately, in scenarios 2 and 4, no insects can ever enter the domain for the initial condition specified above, because  $w_i > w$  over some depth below the updraft cores. Therefore, in the updraft regions in the lower CBL in these scenarios, we set  $w_i$  to zero where  $w_i > w$ , i.e., the insects do not respond to an updraft until they are carried up in it. In reality, microinsects may have to fly up a little to enable the migration from the atmospheric surface layer ( $\approx 10$  m deep) into the CBL. However, even in the surface layer, they tend to be assisted by small buoyant eddies, as shown by laboratory experiments with aphids (Isard and Irwin 1996).

## Results

The first scenario (Figs. 1a and b) confirms that floating particles quickly become dispersed in the CBL, as has been observed for instance for pollutants in the CBL. The value of the eddy diffusivity used here ( $K = 10$  m<sup>2</sup>/s) is representative of air turbulence (e.g., Holton 1993), and random motion of insects will make this dispersal even faster. In this scenario, the maximum concentration anywhere is constrained by the concentration near the ground ( $c = 1/\text{m}^3$ ). After 45 min, the insect concentration in updrafts is still larger than in downdrafts (Fig. 1b), but at 70 min, insects have become rather evenly distributed across the CBL (data not shown). Thus, in this scenario, there would be no echo plumes in the CBL. After 45 min, there is still a small positive correlation between insect concentration and vertical air motion (Fig. 1c). In the model, that correlation disappears by 70 min, as insects gradually become dispersed more uniformly. In the real world, this mixing is probably more rapid because the flow field is not steady: thermals decay within  $\approx 1$  h, and new thermals build through the debris plume of old ones.

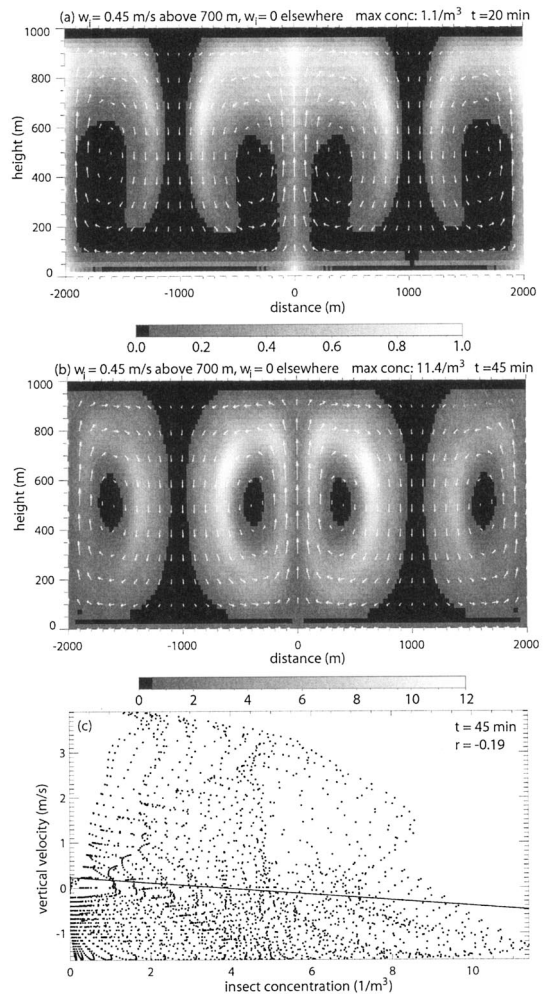
Particles that all continuously subside (the dead particle scenario; Fig. 2) do not necessarily disappear from the CBL after some time. They can remain in the



**Fig. 2.** Insect concentrations in a hypothetical, steady airflow field (a) at  $t = 20$  min and (b) at  $t = 45$  min. (c) Scatter plot of insect concentration versus vertical air motion for the insect distribution shown in b. In this scenario, insects descend at a constant speed ( $w_i = 0.45$  m/s) under any ambient air temperature (the dead particle scenario).

air in a steady state, as long as the vertical air motion locally exceeds the particle fallspeed and there is a low-level source of particles. That enables a local upward particle flux. These particles will exist in higher concentrations in updraft regions, not just early in the simulation, but at all times. They tend to concentrate more at the level where the fallspeed equals the updraft speed. In our simulation, that “equilibrium” level happens to be around 700 m. Large concentrations tend to build up there in time, because in our idealized flow field, the diffluent is small in the updraft at 700 m. In reality, any equilibrium level is short-lived because thermals are quite transient. Particles also concentrate in the low-level entry region of updrafts.

If a downward insect response is only found in the upper CBL (the temperature threshold scenario; Fig.



**Fig. 3.** Insect concentrations in a hypothetical, steady airflow field (a) at  $t = 20$  min and (b) at  $t = 45$  min. (c) Scatter plot of insect concentration versus vertical air motion for the insect distribution shown in b. In this scenario, insects only descend (at a speed  $w_i = 0.45$  m/s) where it is too cold, above a certain height, here 700 m (the temperature threshold scenario).

3), the maximum insect concentration at 45 min is about 11 times larger than that in the source region near the ground. In other words, well-defined insect plumes appear to form. However, the largest concentrations occur in the upper downdrafts. The updraft cores become mostly devoid of radar scatterers. As a result, there is a slightly negative correlation between insect concentration and vertical air motion at  $t = 45$  min (Fig. 3c). Clearly the choice of threshold temperature or height (above which insects stop flying) of 0.7 of the CBL depth ( $z_i$ ) is an arbitrary one; in reality, such a threshold is species-dependent and may be affected by other factors such as insect age and insolation. In any event, a negative correlation is found not only for a threshold height of  $0.7z_i$  but also for a range of heights between  $0.5$  and  $0.8z_i$ . The negative corre-

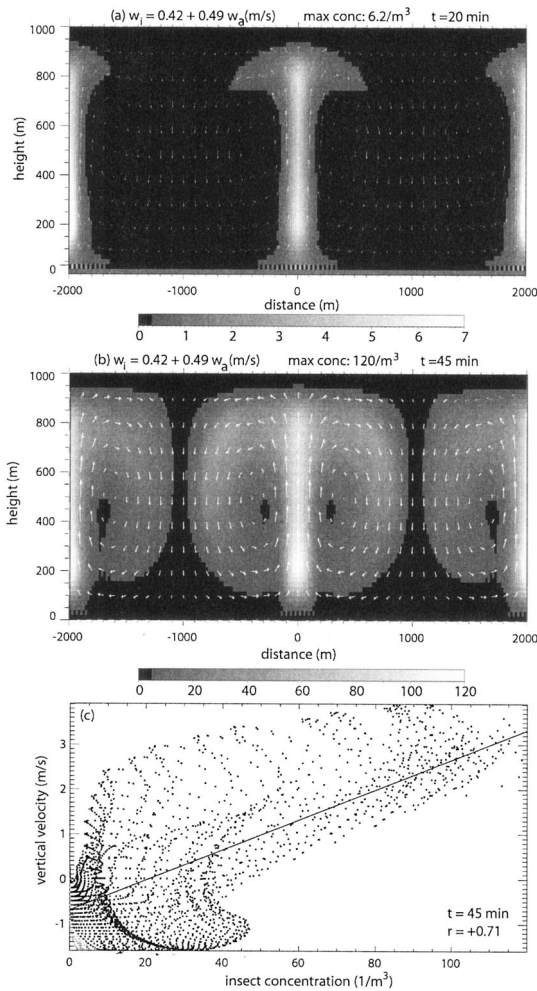


Fig. 4. Insect concentrations in a hypothetical, steady airflow field (a) at  $t = 20$  min and (b) at  $t = 45$  min. (c) Scatter plot of insect concentration versus vertical air motion for the insect distribution shown in b. In this scenario, the insect response is a function of vertical air motion (the updraft opposition scenario).

lation is strongest for  $0.6z_i$  ( $r = -0.26$ ). Whatever the threshold temperature or height, the negative correlation is contradicted by the observations (see Fig. 7 in Geerts and Miao 2005).

Sustained large insect concentrations in updraft regions can only build up if the rate of opposition increases with updraft speed (Fig. 4). Larger concentrations are found in updrafts than in downdrafts in both the dead particle (Fig. 2) and the updraft opposition (Fig. 4) scenarios, but differences develop in the early stages. After 20 min, insects have spread further in the CBL in the no-response case (Fig. 2a) and have congregated more in the updrafts in the updraft-dependent response scenario (Fig. 4a). After 45 min, the concentration peaks at  $12/m^3$  in the former case (Fig. 2b) and at  $120/m^3$  in the latter (Fig. 4b). In other words, well-defined insect plumes that are co-located

with updrafts do develop only when insects oppose the updrafts. Assuming a background concentration of  $1/m^3$  after 45 min and assuming that all insects are of the same size, the reflectivity in plumes would be  $11 \text{ dB}\eta$  higher than in the background in the dead particle scenario (Fig. 2b) and  $21 \text{ dB}\eta$  higher in the updraft opposition scenario (Fig. 4b). Observed reflectivity differences between plumes and the background are  $10\text{--}30 \text{ dB}\eta$  (e.g., Figs. 2 and 4 in Geerts and Miao 2005, see Wilson et al. 1994, Russell and Wilson 1997). Also, a stronger positive linear correlation between concentration and vertical air motion is found in the updraft opposition scenario (Fig. 4c;  $r = +0.71$ ) as opposed to the dead particle scenario (Fig. 2c;  $r = +0.29$ ). This clear positive correlation is consistent with observations (Figs. 7 and 8 in Geerts and Miao 2005).

A simpler, more intuitive model can be devised to show that downward flyers can be sustained in the CBL and that they occur in larger concentrations in updrafts, especially when their downward motion increases with updraft speed. Assume just two flow columns: a  $1.0 \text{ m/s}$  updraft in 10% of the CBL domain and a  $-0.11 \text{ m/s}$  compensating downdraft in the remaining 90% of the area. This reflects the observed skewness of the vertical velocity distribution, although in an exaggerated way. Air mass continuity is satisfied in this example, with no net vertical motion at the CBL top. According to the updraft opposition scenario, insects rise relative to the ground at  $0.09 \text{ m/s}$  in the updraft and subside at  $-0.48 \text{ m/s}$  in the downdraft. Therefore, the CBL experiences an insect influx in the updraft region and an insect outflux in the downdraft region. Insect concentrations can increase or decrease in time, depending on the balance between influx and outflux. A steady state is achieved if influx equals outflux. In this case, the insect concentration is 48 times larger in the updraft than in the downdraft. If a constant fallspeed of  $0.45 \text{ m/s}$  is assumed (the dead particle scenario) for the same updraft/downdraft pair, the insect concentration in the updraft is still larger than in the downdraft, but only nine times larger.

### Discussion

**Implications and Limitations of the Numerical Experiment.** Geerts and Miao (2005) have shown that the radar scatterers tend to subside in the CBL that develops on sunny days in the warm season. These scatterers, mostly microinsects, subside faster in updrafts. The theoretical experiment presented herein shows that this flight behavior explains the very existence of plumes of high microinsect concentrations in the CBL and the collocation of these plumes with thermals of rising air. Apparently, insects tend to remain in a thermal as long as it remains active. The opposition to updrafts also explains the existence of long-lived radar fine-lines in belts of sustained air mass convergence, such as a cold front (Wilson and Schreiber 1986) or a sea breeze front (Drake 1982).

The numerical simulations are a highly simplified version of reality in that they ignore the transience of plumes, three-dimensional effects, wind shear (Symmons and Luard 1982), and possible size selectivity (e.g., larger insects could be relatively more common in updrafts). However, they confirm that insect concentrations in regions of sustained low-level convergence can readily exceed the background value by more than an order of magnitude. They show that insects can become trapped in a thermal as long as the thermal remains buoyant. This explains why plumes are so apparent on radar displays of the CBL and why they rapidly "collapse" in the late afternoon.

The tendency for CBL echoes to subside has also been detected in ground-based profiling radar data, both at 33-cm (e.g., Angevine 1997, Lothon et al. 2002) and at 8.6-mm wavelengths (Martner and Moran 2001). Our study shows that microinsects do not subside at their "terminal fall velocity," i.e., a fallspeed that is a function of their size and weight and independent of ambient conditions. Rather, we find that microinsects oppose the updrafts in which they are embedded. They are still carried upward, but their opposition clearly increases with updraft strength. This finding corroborates a wealth of evidence in the literature supporting the biotic nature of these clear-air scatterers (e.g., Gossard 1990, Russell and Wilson 1997).

**Questioning the Air Temperature Control Theory.** As discussed above, it is well established in the literature that insect flight behavior is sensitive to air temperature. Our numerical simulations suggest that, if microinsects only subside in the upper CBL in response to low temperatures, plumes tend to be ill-defined and they tend to occur in downdrafts, which contradicts observations. The air temperature control theory seems to be especially unlikely in the cases examined in Geerts and Miao (2005), simply because the temperature in the coolest CBL regions, near the CBL top, remained  $>17^{\circ}\text{C}$  on all 4 d (29 May, 3 June, 6 June, and 17 June 2002), according to aircraft-based measurements. The threshold temperature that immobilizes microinsects is species-dependent, and even for a single species, a range of temperatures applies over which the insects first slow down and become immobile (Johnson 1974, Schaefer 1976). Temperature thresholds in the literature generally apply to macroinsect species; for microinsects, they seem to be generally below  $20^{\circ}\text{C}$ . For instance, aphids are found at air temperatures down to  $12.5^{\circ}\text{C}$  (Isard et al. 1990). Even for the more thermophilic insects, only a thin layer near the top of the CBL would be cool enough to allow insect fallout on the four flights analyzed in Geerts and Miao (2005). It should be noted that the temperatures encountered on these flights are not exceptional. Thus, by extension, the unlikelihood of the temperature control theory applies generally to the central Great Plains during the warm season. Clearly we do not question how microinsect flight is affected by low temperatures. Temperature undoubtedly plays a major part in insect migration. We argue that temperature alone does not control the flight and clustering of microinsect in the CBL.

A direct insect response to vertical air motion, however, seems rather unorthodox. The updraft opposition theory evokes three questions. How do microinsects sense vertical air currents? How do they oppose updrafts so effectively? And finally, why do they oppose updrafts? The first question is in regard to insect physiology and is beyond the scope of this study. One clue could reside in the rapid change of air pressure with height, a principle that has long been used in altimetry. Apparently, the Johnston's organ on the antennae of insects in the Diptera family accurately measures barometric pressure, which is essential to flight orientation (Johnson 1974). The two remaining questions are addressed speculatively.

**How Do Microinsects Oppose Updrafts so Effectively?** Insects can fight an updraft either by beating their wings heading down or by folding them and falling. They may also become immobile with their wings unfolded, but this increases the aerodynamic drag and results in a slower sedimentation rate. The relative speed of free fall versus active flight depends on insect size (the Reynolds number). Thomas et al. (1977) studied the fall behavior of aphids, whose average mass is  $\approx 0.5$  mg. They showed that aphids can fly downward at speeds of  $\approx 0.7$  m/s. When they are immobile, their fallspeed ranges from 0.8 (wings open) to 1.8 m/s (wings folded). Larger insects fall only slightly faster. The largest ones in one study (Wellington 1945) weighed 24 mg and fell at  $\approx 2.3$  m/s. In any event, the proposed biotic response should be verified, and methods of downward flight need to be analyzed, for instance, in a relatively tall wind tunnel flight chamber, in which the air pressure decreases hydrostatically with height. Wind tunnel experiments with aphids (Isard and Irwin 1996, Hardie and Powell 2002) have been performed, but these tunnels lack vertical depth and air pressure control. A sufficiently tall wind tunnel may be prohibitively expensive. In situ measurements of insect movement and air motion on a high tower may be more revealing.

**Why Do Microinsects Oppose Updrafts?** Does the tendency of microinsects to oppose updrafts have an "adaptive" advantage in terms of species survival and reproduction? Our observations and simple numerical experimentation have shown that this behavior increases their concentrations in updrafts, so they should remain airborne longer. Microinsects, or "aerial plankton" as they have been called (Drake and Farrow 1989), do not feed in regions of atmospheric convergence and upwelling, unlike oceanic plankton, which feeds and grows in upwelling nutrient-rich waters. To the contrary, the observed behavior of microinsects may negatively affect their survival chances because their higher densities in updrafts makes them easier targets for aerial predators such as swifts. It is well established that the fundamental reason why microinsects become airborne above the vegetation canopy is to relocate their population and colonize a new habitat, generally because of population pressure or diminishing resources in the old habitat (e.g., Isard and Gage 2001).

One can argue then that the observed behavior is a poor adaptive strategy; that microinsects inadvertently become embedded in an updraft and instinctively oppose it, not knowing that the CBL is trapped, fearing that they may freeze to death in a thunderstorm updraft. Basically this argument makes the behavior of microinsects in an updraft analogous to that of an inexperienced swimmer caught in a rip current. It is difficult to conceive that millions of generations of insects have never learned to take advantage of the thermal circulations in the CBL. Certainly local dispersal, away from the thermal that the insects ride, would be more efficient if they do not oppose the updraft, but rather go with the flow. The chances that a thermal updraft is not blocked by a "lid" at the top of the CBL but rather grows into a thunderstorm, are very slim, probably too slim to develop an adaptive evolutionary strategy.

However, if the objective is not to "disperse" but rather to "relocate" a population, the observed strategy has a clear adaptive advantage. That is, by opposing updrafts, the bulk of the population remains airborne longer and can travel further, as a group, with the prevailing horizontal airflow. Presumably less energy is expended settling down in an updraft than trying to recover from an encounter with a downdraft. For weak flyers, this strategy is especially relevant because it allows them to travel long distances, which is often required because of the large distances that may exist between suitable habitats. A contributing meteorological factor is that winds in the daytime unstable boundary layer are considerably stronger than those in the nocturnal stable boundary layer. In the cases studied here, the average wind in the CBL ranged from 4.9 (29 May) to 7.7 m/s (17 June), implying a displacement of 18–28 km in 1 h. This theory is consistent with the diurnal variation of the movement of some microinsects measured in croplands. For instance, western corn rootworm larvae tend to leave the fields between 1000 and 1200 hours local time to take advantage of the unstable atmospheric conditions that facilitate flight over a longer distance (Isard et al. 2000). So rather than being inexperienced swimmers, microinsects appear to be expert paragliders.

In summary, Geerts and Miao (2005) documented that radar scatterers tend to oppose upward air currents (updrafts) in the CBL at a rate that is remarkably proportional to the updraft speed. This opposition, referred to as the insect response, constitutes definitive evidence that the scatterers are biotic, probably mostly weakly flying microinsects. In this paper, a simple numerical simulation of a steady-state airflow field and insect concentration in the CBL was used to show that the observed flight behavior of microinsects explains the existence of well-defined insect plumes in an otherwise well-mixed CBL and the tendency of these plumes to occur in thermals of rising air. It also explains the growth of insect plumes in the morning hours and their rather sudden disappearance in the late afternoon, several hours before sunset, when surface heating diminishes and thermals weaken and vanish.

Other studies have proposed that the response of insects to being lofted high into the CBL is controlled by air temperature. Our numerical simulation shows that such temperature-sensitive responses do not yield the observed correlation between insect concentration and vertical air motion. Relatively weak plumes do occur in this scenario, but they are located to the side of the heads of thermals. We hope that our findings stimulate further observations of microinsect flight behavior in the laboratory or on a tower and further research into the physiological methods of the observed insect response.

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