Layers of nocturnal insect migrants at high-altitude: the influence of atmospheric conditions on their formation

Curtis R. Wood, Suzanne J. Clark*, Janet F. Barlow and Jason W. Chapman†

*Department of Meteorology, University of Reading, Earley Gate, Reading, Berkshire, RG6 6BB, UK; *Biomathematics and Bioinformatics Department, Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK; and †Plant and Invertebrate Ecology Department, Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK*

Correspondence: Curtis Wood. Tel: +44 118 378 6721; fax: +44 118 378 8905; e-mail: c.r.wood@reading.ac.uk

Running title: Biometeorology of nocturnal insect layers

Abstract

1. Radar studies of nocturnal insect migration have often found that the migrants tend to form well-defined horizontal layers at a particular altitude.

2. In previous short-term studies, nocturnal layers were usually observed to occur at the same altitude as certain meteorological features, most notably at the altitudes of temperature inversions or nocturnal wind jets.

3. Statistical analyses are presented of four years' data that compared the presence, sharpness and duration of nocturnal layer profiles (observed using continuously-operating entomological radar) with meteorological variables at typical layer altitudes over the UK.

4. Analysis of these large datasets demonstrated that temperature was the foremost meteorological factor persistently associated with the presence and formation of longer-lasting and sharper layers of migrating insects over southern UK.

Keywords

Insect layering, nocturnal boundary layer, temperature inversion, entomological radar, differential advection.

Introduction

Long-range windborne migrations of insects are of substantial economic importance, because some migrants are pests of agriculture (Pedgley, 1993; Drake & Gatehouse, 1995) or vectors of pathogens affecting humans, their livestock and crops (Reynolds *et al.*, 2006), as well as being of considerable intrinsic interest. Remote sensing techniques, such as entomological radar, are the only methods of unobtrusively collecting data on high-flying macro-insects (those weighing more than about 10 mg) while they are actually engaged in migration (Chapman *et al.*, 2003).

The phenomenon generally termed 'layering'—where a large proportion of the aerial population of migrants at any one time are concentrated at a particular height or narrow range of heights—frequently occurs in all areas of the world that have been studied (Drake & Farrow, 1988; Burt & Pedgley, 1997; Reynolds *et al.*, 2005). The majority of case studies have observed nocturnal layers of insects, and have attributed their formation to particular meteorological variables (Drake & Farrow, 1988 and references therein; Hobbs & Wolf, 1989, 1996; Beerwinkle *et al.*, 1994; Riley *et al.*, 1995; Feng *et al.*, 2003; Reynolds *et al.*, 2005; Wood, 2007). In most cases, nocturnal layers have been located either at the top of temperature inversions, or in the region of local wind speed maxima such as low-level nocturnal jets (Drake & Farrow, 1988; Reynolds *et al.*, 2005; Feng *et al.*, 2004a,b; Wood *et al.*, 2006). In case studies and field campaigns, detailed analyses are typically performed of vertical profiles and temporal evolution.

However, to gain further understanding of the meteorological factors involved in the initiation and maintenance of nocturnal layers, it is necessary to move beyond the typical short-term case-study approach of examining just a few very clear-cut examples. What is required is the systematic analysis of a long-term dataset of contemporaneous insect density-height profiles and associated meteorological variables over the same height range and at the same locality. Until recently this was impossible, as all radar entomology field studies had been short-lived, and the frequent direct measurement of meteorological variables is impractical at most localities (measured data from radiosonde releases are temporally and spatially too sparse to be of use in anything but case studies). However, two technologies have for the first time provided solutions to these problems. First, continuously-operated vertical-looking entomological radars (Chapman *et al.*, 2003) have amassed data on macro-insect density-height profiles over many years. Second, meteorological data from the range of heights over which insect layers exist has been made available for columns above the radar sites via the UK Met Office's operational mesoscale Unified Model. Thus, we are uniquely placed to carry out these long-term systematic analyses of the association of insect layers with a range of meteorological variables.

Although some studies have detected layers at altitudes below 200 m (Drake and Farrow, 1988), analysis of scanning radar data (which only had non-sampled heights of altitudes 0–100 m) showed that nocturnal layers were most common at 300–600 m above ground, at least during 44 summer nights in New South Wales (Drake and Rochester 1994). In the UK, vertical-looking radar studies over many summers detected the peak range as 200–500 m above the ground between 20:00 and 22:00 UTC (Wood *et al.*, 2009); indeed, this height-band and time-period has been termed the 'critical region' for the initiation of nocturnal layers (Wood, 2007; Wood *et al.*, 2009). It is in this region that we suggest that meteorological conditions play a critical role in the formation of nocturnal layers. Hence, in the present study we analyse the relationships between meteorological variables in this critical region with the duration and sharpness of nocturnal layers of migrating macro-insects over the UK. These nocturnal layers are a frequent phenomenon during the summer months, and are primarily composed of large insects in the mass range between about 50 and 200 mg

(Reynolds *et al*., 2005; Wood *et al*., 2009). The only insects in this mass range captured at high-altitude are noctuid moths (Chapman *et al*., 2004, 2008b), and thus one might infer that the nocturnal layers are predominately composed of this group. The most abundant migratory species that make up the UK layers—such as *Autographa gamma*, *Noctua pronuba* and *Agrotis* spp. (Wood *et al*., 2009)—have the potential to be important agricultural pests and are capable of migrating hundreds of kilometres in a single night's flight (Wood *et al*., 2006; Chapman *et al*., 2008a,b). Smaller-sized insects in the layers are likely to include other highly numerous nocturnal migrants, including crop pests like the diamondback moth *Plutella xylostella* (Chapman *et al*., 2002a) and natural enemies like the green lacewing *Chrysoperla carnea* (Chapman *et al*., 2006). A greater understanding of the mechanisms of layer-formation will therefore be important for predicting the long-range windborne movements of pest insects and their natural enemies.

Materials and methods

Meteorological data

The operational numerical weather-prediction model of the UK Met Office—the Unified Model (UM)—provided the meteorological data used in this study (Cullen *et al.*, 1997; Essery *et al.*, 2001; Lock *et al.*, 2000). The UM is non-linearly spaced in the vertical, but has three model levels within the heights identified as critical for layer formation (200–500 m). The profiles of meteorological variables were interpolated between horizontally separated grid-points to specific sites of interest (i.e. Rothamsted and Malvern) and were available at hourly resolution (on the hour). Although the data is based on physical equations and has been the subject of validation studies (Edwards *et al.*, 2006; Lock *et al.*, 2000, 2003; Wood, 2007), for the present study an additional validation was performed. Seventeen stable UM profiles were examined to assess the performance of model data in the nocturnal boundary layer (NBL), as compared with radiosonde releases from Cardington Airfield (UK Met Office, 52.10 °N, 4.20 °W) and Larkhill (51.20 °N, 1.80 °W) between 11 and 245 minutes after sunset. It is at these times that layering is mostly likely to occur (Wood *et al.*, 2009).

In this study, focus is made upon a set of key meteorological variables reported repeatedly in the case-study literature as likely determinants of nocturnal insect layer sharpness (see Table 1 for list of variables). Turbulence is represented by the gradient Richardson number, *Ri*, which is proportional to the ratio of buoyant to shear production of turbulent energy, and calculated as $Ri = (g/\bar{\theta})(\Delta\theta/\Delta z)/(\Delta u/\Delta z)^2$; where g is acceleration due to gravity [m s^{-2}], z is height [m], u is wind speed [m s^{-1}] and θ is potential temperature [K]. Mean values of meteorological variables were taken in the critical region, in the case of 'simple' variables this meant twelve elements comprised the mean: three hours of data (20, 21 and 22 hours UTC) at four model heights (190, 300, 440 and 600 m). Where gradient variables were used, only nine elements comprised the mean since gradients were not available at model levels and thus had to be calculated at half-levels (245, 370 and 520 m). A jet sharpness variable, j, was calculated for each profile: the ratio of the wind speed at wind-speed maximum to the minimum wind speed at greater heights (but with a one kilometre maximum height imposed); a monotonically increasing wind-speed with height gives unity, whilst greater j values are returned as the jet becomes sharper in profile (NB. since at low levels there is always a positive gradient in wind speed with increasing height, j was defined with respect to the wind speeds at high-altitude and not, say, ground-level wind speed).

Wind direction is a circular variable and thus for analysis, the wind vector was decomposed into the conventional u_{east} and u_{north} (analogous to Fisher, 1993): which are positive eastwards and northwards respectively (convention: flow from the west is termed westerly [or eastward], and flow from the south is termed southerly [or northward]).

It is worth noting that meteorological variables are inter-related and thus care should be taken in interpreting any results where they are regressed in the same analyses; in the present cases, their correlation coefficients are noted in Wood (2007).

Radar data

Data were obtained from vertical-looking insect-monitoring radars which have been running since 1999 at two sites in the UK: Rothamsted and Malvern (51.81 °N, 0.36 °W and 52.13 °N, 2.33 °W, respectively). They provide instantaneous vertical profiles of insect aerial density over virtually all high-altitude migration altitudes to be expected over the UK, with the proviso that only insects > 15 mg are detectable over the entire sampling range. Data are recorded for a 5-minute sampling period that is repeated every fifteen minutes, 24 hours a day, thus providing 96 vertical profiles per day. Full details of the radar system, its mode of operation and analysis protocols (including target identification procedures to deal with non-insect targets, such as precipitation, radar chaff, birds and bats) have been described elsewhere (Smith *et al.*, 1993, 2000; Chapman *et al.*, 2002b, 2003).

To assess the form of profile exhibited in each sampling period, the 'layer quality' (LQ) classification (Reynolds *et al.*, 2005) was utilised to categorise each profile. Briefly, LQ values range from 0–7 (integers), layers are detected by analysing an increase in number concentration in the vertical profile; values 4 to 6 represent layers of increasing sharpness in form (and LQ = 7 is a possible layer under conditions of high insect density when inter-target interference can occur). For this long-term study of nocturnal layers, an extended classification scheme was defined and termed 'nocturnal layer quality' (NLQ). A single NLQ value is given for each night, and is calculated by summing the LQ values in the range 4–6 over the period 21:00–23:59 and then dividing by twelve (the number of profiles in that period). An NLQ value of 0 is returned for occasions with no layering at all, 6 is returned for a sharp layer occurring over the entire 21:00–23:59 period, and mid-range values indicate either short-lived sharp layers or longer-lived layers of weaker form. Examples of six nights' radar data for different NLQ values have been produced (Appendix).

Statistical analysis

Radar data were analyzed from the three summer months (June, July and August) in four consecutive years (2000–2003) at both radar sites. Thus 736 'events' (368 nights replicated at two sites) were available for analysis; however, the availability of UM meteorological data reduced that to only 539 events.

For the main body of analyses conducted in this paper (concerned with layer sharpness and duration), the dataset was further reduced—to 412 events—to exclude occasions where there was almost no nocturnal aerial insect activity at all (e.g. due to rain). The insect activity threshold was set to exclude occasions where the total number of detected insects was less than 75 during 21:00–23:59 (NB. the mean summertime insect total during 21:00–23:59 was 391 insects).

A binary analysis approach was taken to assess if there were any statistical differences of individual meteorological factors between layered and non-layered events (binary layer presence defined as NLQ > 1). The 412 events were split into layered profiles (59 events) and weakly- or non-layered profiles (353 events). Mean, or median, meteorological factors in the critical region during layered and non-layered occasions were compared for binary later presence/absence. The null hypothesis was that the means were the same in each population of layering and non-layering events; refutation of the null hypothesis thus indicated that the relevant meteorological factor might have been associated with layered occasions. However, due to the correlation of many meteorological factors with each other, a significant relationship between a particular meteorological factor and strong layering does not prove a causative effect. Rather, it indicates that this factor might have a role to play in layer formation, and is worthy of further analysis.

To discover the relationship between meteorological variables and NLQ (layer sharpness and duration), cases were excluded where there was no layering at all (defined by NLQ = 0): this reduced the number of events in the sample from 412 to 279. First, nightly NLQ values were linearly regressed on the eleven meteorological variables in turn. Second, potential interactions were investigated between subsets of the meteorological variables selected on the basis of the regression results. The chosen variables were grouped into two or three categories (Table 1), determined so that wherever possible an approximately equal number of replicates occurred for each category. Where applicable, the ranges of category variables were chosen to provide clear distinctions between physical phenomena: (*i*) $Ri > 1$ is a higher-end threshold for cessation of turbulence; (*ii*) wind jet was split into jet presence or absence (presence based on $j > 1.1$). The variance in NLQ that could be explained by each of seven pairs of categorised meteorological variables in the critical region (the factors) was then investigated using two-way ANOVA. Temperature was always chosen as one of the pair of factors since it clearly explained the largest amount of variance in NLQ (following the linear regression results, below). For the second of each pair, seven factors were chosen based on either a high degree of variance explained in the linear regressions, or because of strongly reported associations with layering in published studies. Most meteorological variables used in the analysis are not independent, and therefore there will be some variance in NLQ that could be assigned to two different factors. Thus when accounting for variance in NLQ caused by two meteorological variables, the results are dependent upon the order in which variables are fitted in the analysis. For this reason, and because replication was unequal for each combination of the two categorised variables, the "AUNBALANCED" GenStat procedure was used (GenStat® Version 7; Payne *et al.*, 2003), which allowed the two factors to be added sequentially in both orders to assess their effects in the presence and absence of the other variable before assessing their interaction.

It is worth re-stating here that the analyses in this paper are not concerned with matching vertical structures of insect concentrations and their temporal evolution to meteorological variables. The focus of the current study is a broader analysis, concerned with the following questions: (*i*) Are meteorological conditions different between occasions with and without layering? (*ii*) Which meteorological conditions at typical layer height are correlated with longer-lived and sharper layers?

Results

Validation of meteorological data

When compared to the radiosonde releases, the UM predicted the altitude of the temperature inversion correctly on 15 of the 17 occasions examined, with a mean error of just 0.6 °C in inversion-top temperature. Furthermore, the presence of a jet was correctly predicted on 15 of 17 occasions, with a mean underestimate of the jet speed of 1.4 m s^{-1} compared to the radiosonde data. The mean values of various variables at 200–500 m above ground level were analysed to assess the performance of the UM at typical insect layer altitude (Table 2). The only variable with a significant error bias was static stability, which corroborates the previous finding that the UM usually produces profiles that are too highly statically stable, i.e. they have a positive potential temperature gradient (Edwards *et al.*, 2006). The errors of the other estimated variables were not significant (Table 2). We are thus confident that the meteorological data provided by the UM is a very good surrogate for actual observations—and, as such, suitable for our analyses of the meteorological factors associated with insect layering.

Aerial insect abundance

Nocturnal layers are generally observed immediately following a conspicuous increase in high-altitude insect activity at dusk (Wood *et al.*, 2009). Thus it follows that layering will be detected most frequently when the aerial insect number-density is large. Not surprisingly therefore, total insect numbers (in all radar range-gates during 21:00–23:59) were greater (844±170, 95% C.I.) for layered cases compared to non-layered cases (134±19, 95% C.I.).

For the 539 cases with entomological and meteorological data (see *Statistical analyses* above), a two-way ANOVA was conducted where NLQ was the response variate, and categorised factors were temperature and total insect numbers. Both temperature and total insect numbers explained variance in NLQ, whether accounted for first or second in the analysis[*]. This indicates that both increased total insect numbers and warmer temperatures were associated with increased NLQ values.

The remaining analyses in this paper were performed to investigate the effect of meteorological variables on layering *given* that aerial insect numbers were relatively numerous: the 412 events with > 75 total insects between 21:00 and 23:59.

Layer presence

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[*] Temperature ignoring targets F=100.5, p<0.001. Temperature eliminating targets F=6.5, p=0.002. Targets ignoring temperature F=367.0, p<0.001. Targets eliminating F=273.0, p<0.001. Interaction F=5.8, p<0.001. Residual df=531.

Table 3 shows the summary of the binary analyses. The mean temperature was higher during layered events than non-layered events by 2.4 °C . Mean RH was 7 % lower for layered profiles; and mean q was higher by 0.4 g kg^{-1} for layered profiles. These results suggest that humidity might explain some of the variation in NLQ. However, humidity and temperature are highly correlated, and so the interaction between humidity, temperature, and NLQ is analysed further with two-way ANOVA (see below). Contrary to expectations, wind speed was in fact 0.7 m s^{-1} *lower* during layered occasions . The median jet intensity was higher by 0.4 during layered events. This indicates that wind does affect the formation of nocturnal insect layers, but that the relationship is not straightforward. There was no significant difference between the medians of layering and non-layering populations for shears of wind speed or direction. Potential temperature gradient and Richardson number were both more stable when layering occurred. The wind direction analyses indicated no effect on layering of the north-south component; but there was a negative relationship with the east-west component: layering was more frequently associated with winds from the east.

Layer sharpness and duration

To discover the relationship between meteorological variables and NLQ (layer sharpness and duration), only values of NLQ > 0 (i.e. those cases with some degree of layering) were included in the analyses. The linear regressions are shown in Figure 1.

Temperature had the strongest correlation with NLQ. Stable (more positive) potential temperature gradients were correlated with increased NLQ. Low relative humidity and high specific humidity were associated with increased NLQ values. Thus these variables were taken forward to the ANOVA interaction analyses.

NLQ did not have significant relationships with wind speed, vertical shear in wind speed, or vertical shear in wind direction. However, higher values of NLQ were associated with increased jet sharpness. Similar to the binary analysis, there was no relationship with the north-south wind component; but there was a negative relationship between the east-west component and NLQ, i.e. layering was more frequent and stronger when the wind was *from* the east. Easterlies were warmer than westerlies ($r = -0.35$, $p < 0.001$, between T and u_{east}). Since there was a relationship with both u_{east} and jet sharpness—and layers have been linked to wind speed in previous studies—wind speed and jet sharpness were taken forward to the ANOVA interaction analyses.

NLQ was unaffected by turbulence, using *Ri* as an indicator. However, since *Ri* is a ratio variable, values of very high magnitude can occur which will distort the distribution and hence relationships are better analysed in category form, such as in ANOVA. *Ri* was thus taken forward to the ANOVA interaction analyses.

Considering the results of the two-way ANOVA (Table 4), regardless of whether the variance in NLQ due to temperature was taken as a first factor (row 1a) or second factor (row 2b), there was always a significant relationship of temperature with NLQ. Only potential temperature gradient had a significant effecton NLQ once variance due to temperature had first been accounted for (row 1b). There was also no evidence that any of the factors had a significant interaction with temperature on NLQ.

When variables (other than temperature) were analysed first (row 2a), the results were largely consistent with the linear regressions. However, these apparent relationships between meteorological factors (other than temperature) and NLQ are probably due to those other factors acting as surrogates for temperature. This is evident when one considers the order in which variance in NLQ is accounted for in the two-way ANOVA analyses; when temperature is taken account of first, the other factors do not explain any significant variance in NLQ (except potential temperature gradient).

Discussion

High abundance of insects at layer altitudes is undoubtedly a pre-requisite for detection of layers and perhaps for their existence[*]. Near-surface meteorology, general synoptic conditions and seasonal factors will presumably all influence the aerial number-density of migrants and thus the strength of the dusk peak, which subsequently effects layering. In the present paper, we have attempted to identify the atmospheric conditions in the critical region that are associated with strong and persistent layering, given that numerous insects are already flying.

It is re-assuring to see that in north-western Europe, our analyses have shown that temperature is the dominant meteorological variable affecting the presence, sharpness and duration of nocturnal layers of large insects; this corresponds well with previous short-term studies (Drake & Farrow, 1988; Feng *et al.*, 2004a,b; Reynolds *et al.*, 2005). Since temperature influences many facets of insect physiology and behaviour (e.g. Carpenter *et al.*, 1981; Drake & Farrow, 1988; Gatehouse, 1997) and considering the fact that, on most occasions, nocturnal UK temperatures will be sub-optimal for insect flight activity, one would expect temperature to be the dominant factor in a hierarchy of meteorological variables that influence high-altitude insect layering.

[*] Although it is worth noting that at low concentrations the LQ system was designed to be sure that a layer was occurring and that the system did not report a layer when just a few individuals were detected (see Reynolds *et al.*, 2005); this gives rise to a small positive link between NLQ and insect concentrations.

Considering that many short-term studies have reported the association of layers with the presence of maxima of meteorological variables other than temperature (Drake & Farrow, 1988; Wood, 2007), it is interesting that in our systematic long-term study, temperature was the only meteorological variable to have a substantial effect on the formation and subsequent sharpness of nocturnal layers of migrating insects. The gradient of potential temperature was the only other variable to remain significant once variance due to temperature had been taken account of; this positive relationship was observed elsewhere (Wolf *et al.*, 1986) and is worthy of further study. It is unclear why this relationship might hold; to speculate: perhaps the more stable air is more conducive to layering because the air is less turbulent (but then there was not a relationship with Richardson number), or perhaps temperature inversions are more likely when the atmosphere is stable and thus layering is more likely since many layers are seen in the warmest air atop temperature inversions.

Linear regression analysis indicated that the presence of a nocturnal wind jet, higher specific humidity and lower relative humidity also promoted the formation and maintenance of nocturnal layers, but this result was not borne out by the ANOVA analyses. In those cases, temperature appeared to be the most important meteorological variable by far in the formation of nocturnal layers of migrating insects.

The relationship with east-west wind was consistent with synoptic summertime flow: winds from the east tend to be much warmer. Consequently once temperature had been accounted for, there was no longer any significant amount of variance explained by east-west winds. Considering the north-south winds, it has been observed that large nocturnal migration events tend to occur primarily in early-season on southerly winds, followed by late-season return migrations on northerly winds (Chapman *et al.*, 2008a,b). Thus the lack of a north-south effect is presumably because both northerly and southerly winds are equally good for mass migrations (and thus are both likely to have lots of nights with lots of activity and strong layers).

One interesting negative result was the complete lack of a relationship between NLQ and wind directional shear in our findings. Studies of passive material with a heterogeneous source at the ground have shown that material typically becomes layered given the presence of a vertical shear of wind direction; this effect is known as differential advection (e.g. Bowen *et al.*, 2000). As there was no evidence that differential advection was responsible for the layers observed in this study, this is consistent with the idea that the source populations of migrants are homogenously distributed over large areas (Taylor, 1973).

The present paper demonstrates the importance of a long-term (rather than case-study) approach for correlating insect layers with meteorological conditions at layer altitudes. This has only been made possible by the long-term deployment of entomological radars, along with the availability of vertical profiles of meteorological data obtained from a weather prediction model. Systematic long-term studies that can go beyond the broad approach of this paper and instead relate vertical structures of insect concentrations and meteorological variables to one another, and study the effect of aerial insect number-density, will result in further insights into the ecology of high-altitude insect migration and layers.

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Appendix

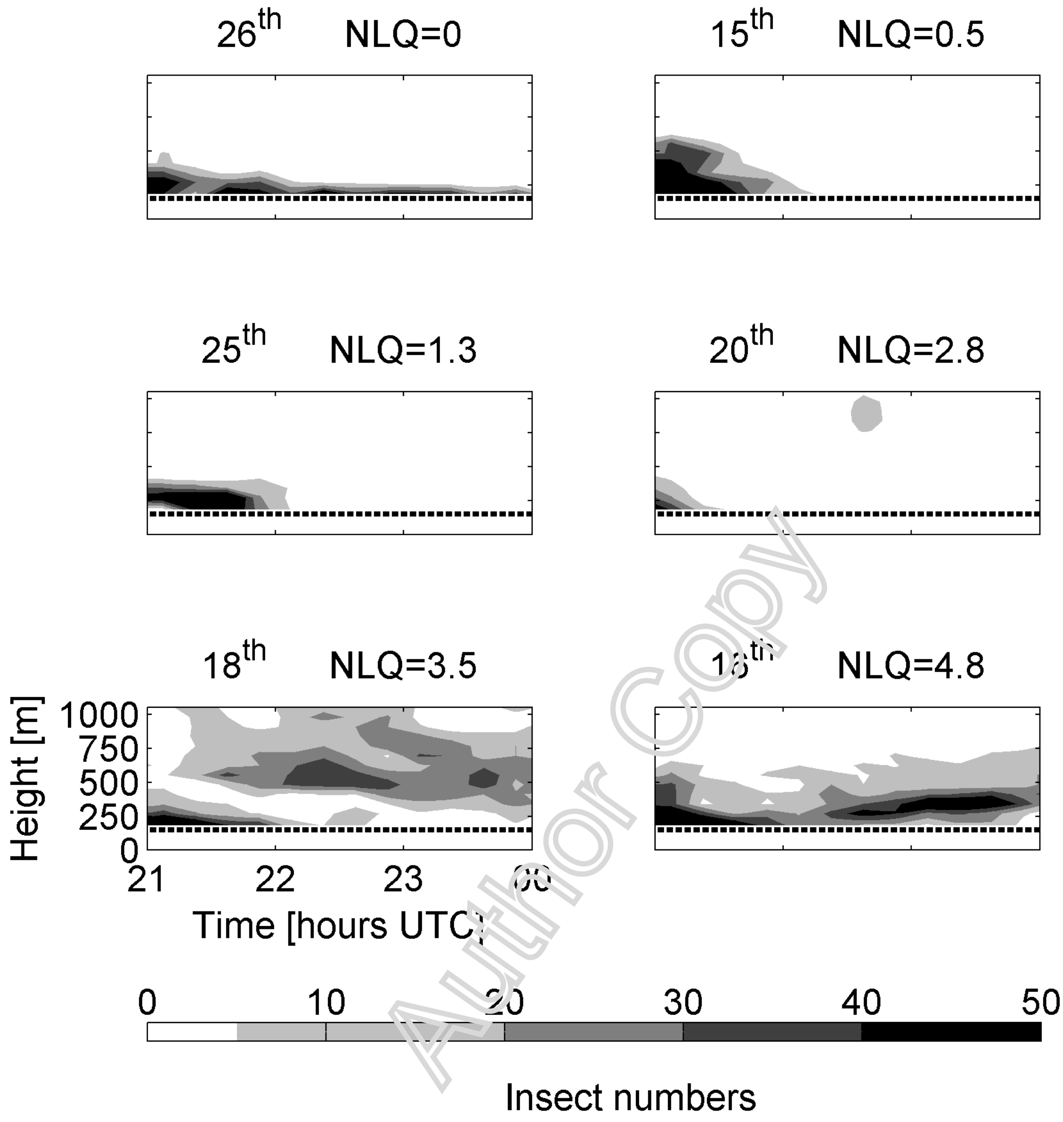

Figure Examples of six evenings' data from the Malvern radar, June 2000. Insect numbers are the number of insects per five minutes per range gate. No radar data were available below 180 m.

References

Beerwinkle, K.R., Lopez, J.D., Witz, J.A., Schleider, P.G., Eyster, R.S. & Lingren, P.D. (1994) Seasonal radar and meteorological observations associated with nocturnal insect flight at altitudes to 900 meters. *Environmental Entomology,* **23**, 676–683.

Bowen, B.M., Baars, J.A. & Stone, G.L. (2000) Nocturnal wind direction shear and its potential impact on pollutant transport. *Journal of Applied Meteorology*, **39**, 437–445.

Burt, P.J.A. & Pedgley, D.E. (1997) Nocturnal insect migration: effects of local winds. *Advances in Ecological Research*, **27**, 61–92.

Carpenter, J.E., Sparks, A.N. & Harrell, E.A. (1981) The effect of temperature on wingbeat frequency and sustained flight on certain Lepidopterous insects. *Journal of the Georgia Entomological Society*, **16**: 451–457.

Chapman, J.W., Reynolds, D.R. & Smith, A.D. (2003) Vertical-looking radar: A new tool for monitoring high-altitude insect migration. *Bioscience*, **53**, 503–511.

Chapman, J.W., Reynolds, D.R., Smith, A.D., Riley, J.R., Pedgley, D.E. & Woiwod, I.P. (2002a) High-altitude migration of the diamondback moth *Plutella xylostella* to the U.K.: a study using radar, aerial netting and ground trapping. *Ecological Entomology*, **27**, 641–650.

Chapman, J.W., Reynolds, D.R., Smith A.D., Smith, E.T. & Woiwod, I.P. (2004) An aerial netting study of insects migrating at high-altitude over England. *Bulletin of Entomological Research*, **94**, 123–136.

Chapman, J.W., Reynolds, D.R., Brooks, S.J., Smith, A.D. & Woiwod, I.P. (2006) Seasonal variation in the migration strategies of the green lacewing *Chrysoperla carnea* species complex. *Ecological Entomology*, **31**, 1–11.

Chapman, J.W., Reynolds, D.R., Hill, J.K, Sivell, D., Smith, A.D. & Woiwod, I.P. (2008a). A seasonal switch in compass orientation in a high-flying migratory moth. *Current Biology*, **18**, R908–R909.

Chapman, J.W., Reynolds, D.R., Mouritsen, H., Hill, J.K, Riley, J.R., Sivell, D., Smith, A.D. & Woiwod, I.P. (2008b) Wind selection and drift compensation optimise migratory pathways in a high-flying moth. *Current Biology*, **18**, 514–518.

Chapman, J.W., Smith, A.D., Woiwod, I.P., Reynolds, D.R. & Riley, J.R. (2002b) Development of vertical-looking radar technology for monitoring insect migration. *Computers and Electronics in Agriculture*, **35**, 95–110.

Cullen, M.J.P., Davies, T., Mawson, M.H., James, J.A., Coulter, S.C. & Malcolm, A. (1997) An overview of numerical methods for the next generation UK NWP and climate model. In: Lin CA, Laprise R, Ritchie H (eds) Numerical methods in atmospheric and ocean modelling: The Andre J. Robert memorial volume. Canadian Meteorological and Oceanographic Society, Ottawa, Canada, pp 425–444.

Drake, V.A. & Farrow, R.A. (1988) The influence of atmospheric structure and motions on insect migration. *Annual Review of Entomology*, **33**, 183–210.

Drake, V.A. & Gatehouse, A.G. (1995) (eds) Insect Migration: Tracking Resources through Space and Time. Cambridge University Press, Cambridge, UK.

Drake, V.A. & Rochester, W.A. (1994) The formation of layer concentrations by migrating insects. In *21st Conference on Agricultural & Forest Meteorology and the 11th Conference of Biometeorology and Aerobiology*, pages 411–414. American Meteorological Society.

Edwards, J.M., Beare, R.J. & Lapworth, A.J. (2006) Simulation of the observed evening transition and nocturnal boundary layers: single-column modeling. *Q. J. R. Meteorol. Soc.*, **132**, 61–80.

Essery, R., Best, M. & Cox, P. (2001) MOSES 2.2 technical documentation. Technical Report No. 30, UK Met Office Hadley Centre.

Feng, H.Q., Wu, K.M., Cheng, D.F. & Guo, Y.Y. (2003) Radar observations of the autumn migration of the beet armyworm *Spodoptera exigua* (Lepidoptera: Noctuidae) and other moths in northern China. *Bulletin of Entomological Research*, **93**, 115–124.

Feng, H.Q., Wu, K.M., Cheng, D.F. & Guo, Y.Y. (2004a) Northward migration of *Heliocoverpa armigera* (Lepidoptera: Noctuidae) and other moths in early summer observed with radar in northern China. *Ecology and Behaviour*, **97**, 1874–1883.

Feng, H.Q., Wu, K.M., Cheng, D.F. & Guo, Y.Y. (2004b) Spring migration and summer dispersal of *Loxostege sticticalis* (Lepidoptera: Pyralidae) and other insects observed with radar in northern China. *Environmental Entomology*, **33**, 1253–1265.

Fisher, N.I. (1993) *Statistical analysis of circular data.* Cambridge: Cambridge University Press.

Gatehouse, A.G. (1997) Behavior and ecological genetics of wind-borne migration by insects. *Annual Review of Entomology*, **42**, 475–502.

Hobbs, S.E. & Wolf, W.W. (1989) An airborne radar technique for studying insect migration. *Bulletin of Entomological Research*, **79**, 693–704.

Hobbs, S.E. & Wolf, W.W. (1996) Developments in airbourne entomological radar. *Journal of Atmospheric and*

Oceanic Technology, **13**, 58–61.

Lock, A. (2003) Boundary Layer Processes, Option 6/8A: the parametrization of turbulent fluxes above the surface. Unified Model Documentation Paper 24, available from the Met Office.

Lock, A.P., Brown, A.R., Bush, M.R., Martin, G.M. & Smith, R.N.B. (2000) A new boundary layer mixing scheme. Part 1: Scheme description and single-column model tests. *Monthly Weather Review*, **128**, 3187–3199.

Payne, R.W., Baird, D.B., Cherry, M., Gilmour, A.R., Harding, S.A., Kane, A.F. & Lane, P.W. (2003) The guide to GenStat® release 7.1. Part 2: Statistics. VSN International, Hemel Hempstead, UK.

Pedgley, D.E. (1993) Managing migratory insect pests—a review. *International Journal of Pest Management*, **39**, 3–12.

Reynolds, D.R., Chapman, J.W., Edwards, A.S., Smith, A.S., Wood, C.R., Barlow, J.F. & Woiwod, I.P. (2005) Radar studies of the vertical distribution of insects migrating over southern Britain: the influence of temperature inversions on nocturnal layer concentrations. *Bulletin of Entomological Research*, **95**, 259–274.

Reynolds, D.R., Chapman, J.W. & Harrington, R. (2006) The migration of insect vectors of plant and animal viruses. *Advances in Virus Research*, **67**, 453–517.

Riley, J.R., Reynolds, D.R., Smith, A.D., Edwards, A.S., Zhang, X.X., Cheng, X.N., Wand, H.K., Cheng, J.Y. & Zhai, B.P. (1995) Observations of the autumn migration of the rice leaf roller *Cnaphalocrosis medinalis* (Lepidoptera: Pyralidae) and other moths in eastern China. *Bulletin of Entomological Research*, **85**, 397–414.

Smith, A.D., Reynolds, D.R. & Riley, J.R. (2000) The use of vertical-looking radar to continuously monitor the insect fauna flying at altitude over southern England. *Bulletin of Entomological Research*, **90**, 265–277.

Smith, A.D., Riley, J.R. & Gregory, R.D. (1993) A method for routine monitoring of the aerial migration of insects by using a vertical-looking radar. *Philosophical Transactions of the Royal Society of London B*, **340**, 393–404.

Taylor, L.R. (1973) Monitoring change in the distribution and abundance of insects. Rothamsted Experimental Station Report for 1973, Part 2. pp 202–239.

Wolf, W.W., Westbrook, J.K. & Sparks, A.N. (1986) Relationship between radar entomological measurements and atmospheric structure in south Texas during March and April 1982. In *Proc. of Entomological Societies of America and Canada, Toronto,* pages 84–97.

Wood, C.R. (2007) The biometeorology of high-altitude insect layers. Ph.D. thesis, University of Reading, UK.

Wood, C.R., Chapman, J.W., Reynolds, D.R., Barlow, J.F., Smith, A.D. & Woiwod, I.P. (2006) The influence of the atmospheric boundary layer on nocturnal layers of noctuids and other moths migrating over southern Britain. *International Journal of Biometeorology*, **50**, 193–204.

Wood, C.R., Reynolds, D.R., Wells, P.M., Barlow, J.F., Woiwod, I.P. & Chapman, J.W. (2009) Flight periodicity and the vertical distribution of high-altitude moth migration over southern Britain. *Bulletin of Entomological Research*, doi:10.1017/S0007485308006548

Table 1: Key meteorological variables considered and threshold values used to group each into discrete categories for ANOVA analysis, with number of replicates (nightly values) in each category.

Variable	categories 1	categories 2	categories 3	replicates 1	replicates 2	replicates 3
Wind speed, u [m s^{-1}]	< 6	$6 \leq u \leq 8.5$	> 8.5	99	106	74
Temperature, T [°C]	< 14	$14 \leq T \leq 16.5$	> 16.5	100	108	71
Relative humidity, RH [%]	< 65	65≤ RH ≤80	> 80	71	134	74
Specific humidity, q [g kg^{-1}]	< 7.2	$7.2 \leq q \leq 8.5$	> 8.5	72	131	76
Potential temperature gradient, $\partial\theta/\partial z$ [K km^{-1}]	< 2.0	$2.0 \leq \partial\theta/\partial z \leq 4.0$	> 4.0	49	137	93
Richardson number, Ri	< 1.0	$Ri \geq 1.0$	-	31	248	-
Jet presence, j	Yes (j > 1.1)	no ($j \leq 1.1$)	-	151	128	-
Eastward wind speed, u_{east} [m s^{-1}]	< 0	$u_{east} > 0$	-	118	161	-

Table 2: Mean errors of the UM-simulated meteorological variables, compared to data from radiosonde releases, in the atmospheric region between 200 and 500 m AGL; with 95% confidence intervals (CI) about the means. Significant error biases are indicated with an asterisk(*).

Variable	**Wind speed** u **[m s^{-1}]**	**Temperature** T **[°C]**	**Relative humidity RH [%]**	**Specific humidity** q **[g kg^{-1}]**	**Potential temperature gradient** $\partial\theta/\partial z$ **[K km^{-1}]**	**Magnitude of vertical shear of wind speed** $\lvert\partial u/\partial z\rvert$ **[m s^{-1} km^{-1}]**	**Jet sharpness** j	**Magnitude of vertical shear of wind direction** $\lvert\partial\Phi/\partial z\rvert$ **[° m^{-1}]**	**Wind direction** Φ **[°]**
Mean	–0.1	–0.2	0.9	0.1	0.04*	–0.01	1.1	0.10	–16
CI	±1.0	±0.4	±8.1	±0.6	±0.03	±0.03	±1.9	±0.29	±16

Table 3: Summary of averages of layered and non-layered factors (using NLQ=1 as the threshold; thus N=59 for layered and N=353 for non-layered). The Mann-Whitney U-test was used where the data were highly skewed (|sk|>1); otherwise, the p-values were obtained using the standard t-test.

Variable	Wind speed u [m s^{-1}]	Temperature T [°C]	Relative humidity RH [%]	Specific humidity q [g kg^{-1}]	Potential temperature gradient $\partial\theta/\partial z$ [K m^{-1}]	Magnitude of vertical shear of wind speed $\lvert\partial u/\partial z\rvert$ [m s^{-1} m^{-1}]	Richardson number, Ri	Jet sharpness j	Magnitude of vertical shear of wind direction $\lvert\partial\phi/\partial z\rvert$ [° m^{-1}]	Eastward wind speed u_{east} [m s^{-1}]	Northward wind speed u_{north} [m s^{-1}]
Skewness	0.46	0.82	–0.42	0.44	3.00	1.03	3.53	7.53	4.02	–0.63	–0.01
Mean (non-layer)	7.8	14.1	75	7.9	0.0029	0.005	346	1.7	0.07	2.98	1.36
Mean (layer)	7.1	16.5	68	8.3	0.0041	0.005	601	2.7	0.09	–0.01	0.30
Median (non-layer)	7.4	13.9	74	7.7	0.0026	0.004	6	1.1	0.04	3.95	1.23
Median (layer)	7.1	15.4	67	8.1	0.0033	0.003	10	1.5	0.04	0.67	0.21
p-value	0.03	<0.001	<0.001	0.01	<0.001	0.06	<0.001	<0.001	0.35	<0.001	0.07
Test statistic	2.15	–7.79	5.37	–2.70	14122	18338	16338	15337	19815	5.77	1.14

Table 4: The F and p values for six unbalanced two-way ANOVAs with explanatory meteorological variables (N=279 for all variables), as specified in Table 1, categorised into two or three discrete groups. In each case NLQ was the dependent variable, and the explanatory categorical variables were temperature and a second factor (as defined in Table 1). Values of NLQ=0 were excluded.

Analysis	**Second factors**						
	u	**RH**	***q***	**$\partial\theta/\partial z$**	***Ri***	***j***	**u_{east}**
1a Temperature factor ignoring second factor	14.8, <0.001	15.6, <0.001	15.2, <0.001	15.0, <0.001	14.6, <0.001	14.7, <0.001	14.9, <0.001
1b Second factor allowing for temperature factor	2.7, 0.71	4.2, 0.72	3.3, 0.65	4.8, 0.01	0.3, 0.57	1.6, 0.30	2.2, 0.137
2a Second factor ignoring temperature	1.4, 0.75	11.9, 0.06	0.7, 0.02	6.9, 0.001	3.7, 0.06	1.7, 0.13	7.2, 0.01
2b Temperature factor allowing for second factor	16.0, <0.001	7.9, <0.001	17.8, <0.001	12.9, <0.001	13.0, <0.001	14.6, <0.001	12.4, <0.001
+ Interaction term	1.4, 0.19	3.6, 0.16	1.9, 0.61	0.4, 0.80	0.2, 0.80	0.3, 0.22	1.8, 0.17
Residual df	270	270	270	270	274	274	274

Figure captions

Figure 1: Linear regression analyses of NLQ values (on all y-axes, see bottom-left plot) on eleven meteorological variables (N=279 for all variables); *r* is the correlation coefficient and p is the observed probability level for the regression F-statistic. Values of NLQ=0 have been excluded.

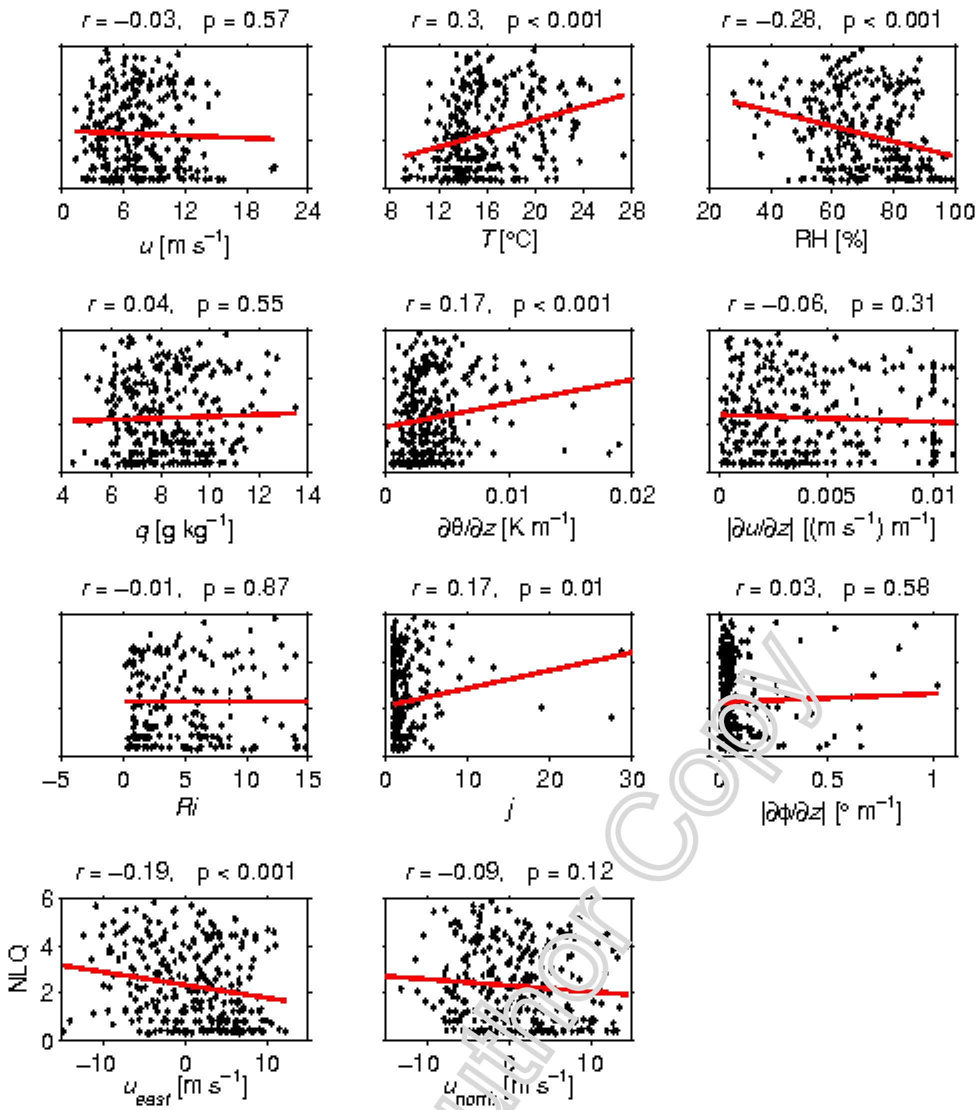

Figure 1: Linear regression analyses of NLQ values (on all y-axes, see bottom-left plot) on eleven meteorological variables (N=282 for all variables); r is the correlation coefficient and p is the observed probability level for the regression F-statistic. Values of NLQ=0 have been excluded.