High-altitude migration of the diamondback moth *Plutella xylostella* to the U.K.: a study using radar, aerial netting, and ground trapping

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Abstract. 1. The high-altitude wind-borne migration of the diamondback moth *Plutella xylostella* in the U.K. in 2000 was investigated (a) by direct monitoring of insect flight by vertical-looking radar and by aerial netting, and (b) through evidence of temporal variation in *P. xylostella* abundance deduced from a network of light traps.

2. Migrating *P. xylostella* were identified by a unique combination of size and shape data derived from the continuously operating vertical-looking radar.

3. Radar-detected migratory overflights correlated significantly with associated peaks in abundance of *P. xylostella* estimated by catches in a U.K.-wide light trap network; however the correlation was stronger when light trap catches were lagged by 1 day.

4. The first notable catches of *P. xylostella* in the U.K. occurred in early May, and were accompanied by migrations over the radar from the east.

5. Radar data and back-tracking indicated that a major wind-borne migration of *P. xylostella* from The Netherlands to southern England took place in early May, and that this was responsible for the establishment of the U.K. population.

6. The origin of early-season *P. xylostella* occurring in Britain is discussed.

Key words. Aerial netting, diamondback moth, flight behaviour, Lepidoptera, light trapping, *Plutella xylostella*, radar entomology, vertical-looking radar, wind-borne migration.

Introduction

The incidence of high-flying insect fauna passing over Rothamsted, Harpenden, U.K. (51°49′N, 0°22′W) has been monitored for the past 3 years. Measurements, made with vertical-looking radar (Smith *et al.*, 1993, 2000), record the displacement vector of individual overflying insects, their altitude, and their radar scattering properties, every 15 min, 24 h a day. The work reported here describes how a subset of these data was used to investigate the migratory flight of the diamondback moth *Plutella xylostella* (L.)

(Lepidoptera: Yponomeutidae). For the first time in a radar study of insect migration, a unique combination of size and shape data embedded in the radar signals was used to identify the target species.

Plutella xylostella is highly migratory, and its seasonal movements have been well documented (French & White, 1960; Lokki *et al.*, 1978; Talekar & Shelton, 1993). It has a cosmopolitan distribution and is believed to be the most universally distributed species of Lepidoptera, occurring wherever crucifers are grown (Talekar & Shelton, 1993). In tropical and subtropical areas, it has continuous generations. By contrast, in the northern- and southern-most parts of its range (e.g. Scandinavia, Canada, northern Japan, southern Argentina), where it is incapable of surviving winter temperatures, outbreaks are entirely the result of regular, long-range immigrations (Talekar & Shelton, 1993).

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In temperate regions, *P. xylostella* may be able to overwinter in small numbers (Marsh, 1917; Hardy, 1938) but it is widely believed that annual occurrences in these regions result largely from wind-borne immigration of adult moths from warmer regions (Talekar & Shelton, 1993). In the U.K., it is usually assumed that if there is a small over-wintering population, it is augmented to a greater or lesser extent by immigration from continental Europe on an annual or near-annual basis (French & White, 1960). Thus, in years when *P. xylostella* is abundant, its high numbers have been attributed to influxes from continental Europe, and in a few years there is no doubt that very substantial immigrations occurred: e.g. 1958 (French & White, 1960), 1966 (Shaw & Hurst, 1969), 1978 (Lokki *et al.*, 1978). The 1958 outbreak, which was the most severe, is the best studied migration event of this species (French & White, 1960; Johnson, 1969; Shaw & Hurst, 1969). There was an enormous influx of *P. xylostella* into the north and east of the U.K. in June and July 1958. Back-tracks indicated that the moths originated in the countries bordering the eastern Baltic Sea, and that they had flown more than 2000 km. The June outbreak of 1966 was attributed to immigration from the same region (Shaw & Hurst, 1969). Although this scenario has been demonstrated only for two exceptional influx years, it has nevertheless come to be assumed as the most probable cause of *P. xylostella* populations in the U.K. (Talekar & Shelton, 1993). That is, high-density U.K. populations generally arise from immigrations from Scandinavia in mid-summer. The focus of this study was to use the radar data (supplemented by aerial trapping and light trap data) to test this assumption and to attempt to determine the balance between putative overwintering and immigration in a more typical year. Thus, the study focused on the origin of the U.K. population in 2000, and in particular on the early-season observations.

Methods

Vertical-looking radar

The study was concerned with data accumulated by the radar during the flight period of *P. xylostella* in the U.K. in 2000. The radar equipment, mode of operation, and analysis capabilities have been described in detail elsewhere (Smith *et al.*, 1993, 2000; Smith & Riley, 1996; Chapman *et al.*, 2002). In brief, the radar senses targets passing through its vertically pointing beam and within 15 height bands (range gates) each 45 m deep. These sampling bands are separated by intervals of 26 m and are set to provide coverage across the altitude range from 150 to 1166 m above ground level (a.g.l.). The amplitudes of any signals captured within the range gates are recorded routinely in digital format for a 5-min period every 15 min, 24 h a day. During the 10-min intervals between recording periods, the signals are analysed automatically using a novel iterative procedure based on their complex Fourier transformations (Smith *et al.*, 1993). If the procedure converges to a solution,

it yields the target's distance of closest approach to the beam's axis of nutation (P), its horizontal speed, displacement direction, and body alignment. A novel feature of vertical-looking radar signals is that they also yield three terms that describe the radar scattering properties of the target, from which its mass and shape can be estimated (Smith & Riley, 1996; Chapman *et al.*, 2002). These seven extracted parameters are then used with other products of the procedure to create a simulated signal, and the correlation between this and the radar return provides a quantitative estimate of how well the model has described the over-flying target (Smith *et al.*, 1993; Smith & Riley, 1996). The parameters, the correlation coefficient (C), the date and time, and the altitude of the target, are all stored for later display and examination. The aerial density of overflying insects is found by calculating the volume sensed by the vertical-looking radar for each target (Chapman *et al.*, 2002). The effective radius of the beam within any range gate is dependent on the mass of the insect detected; for *P. xylostella* ($\approx$1–4 mg), this is $\approx$4 m for gate 1 (Chapman *et al.*, 2002). Aerial densities are expressed in terms of the mean number of insects per $10^7 \mathrm{m}^3$ as calculated for each 5-min sample period. The date assigned to each nocturnal period is that of the evening component (e.g. 1 May is equivalent to 21.00 hours on 1 May to 03.00 hours on 2 May).

Analysis of radar-detected targets was restricted to those with $C > 0.90$ because this showed that the estimates of their parameters were very reliable (Smith *et al.*, 1993; Chapman *et al.*, 2002). Targets with flight trajectories that came no closer than the outer edges of the beam ($P > 0.85$ of a half-power beam width) were also discounted routinely, as the beam gain (sensitivity) beyond this point is not described accurately by the Gaussian function assumed in the analysis routine (Smith *et al.*, 2000).

Selection of P. xylostella-*like targets from the radar data*

Target identification procedures used by vertical-looking radars rely on three potential types of information embedded in the radar signals: estimates of body mass, ratios of radar scattering terms that depend on body shape (Riley, 1985; Chapman *et al.*, 2002), and wing-beat frequency. Of these, estimates of body mass are usually by far the most valuable because they can be compared immediately with the body mass range of the selected species. Use of radar scattering terms is less straightforward because only a few measurements on known species are available, and those that are available suggest that relating the body shape of larger insects to their scattering terms is not always successful (Aldous, 1990). Nevertheless, for smaller species in which body circumference is much less than a radar wavelength, the ratio of the principal scattering terms (σ_{xx}/σ_{yy}) can be expected to rise from unity for spherically shaped insects, to increasingly large values as the ratio of body length to width increases. Thus, in principle, it should be possible to assign vertical-looking radar-detected insects

to functional groups depending on their mass and radar cross sections. Wing-beat frequency data are extractable only if the radar nutation cycle is stopped periodically (Drake *et al.*, 2002), which was not the case in these observations. Thus, identity-related data available from the radar signals themselves were limited to estimates of body mass and the principal scattering terms of individual overflying targets.

In order to determine criteria for the selection of *P. xylostella*-like targets from the bulk of the radar data, *P. xylostella* of both sexes caught in a mercury vapour light trap and an aerial net were weighed, and it was found that their mass range was between 1 and 4 mg (J. Chapman, unpublished). A further selection criterion was that only targets in flight between sunset and sunrise should be included because *P. xylostella* is known to have nocturnal flight activity (Goodwin & Danthanarayana, 1984). Thus, only targets with a mass appropriate for *P. xylostella*, and flying between 21.00 and 03.00 hours were selected for study. A sensitive radar cross-section measurement method (Riley, 1985) was also used to establish the two principal scattering terms (σ_{xx} and σ_{yy}) for a male and female *P. xylostella*. The identity of the radar-detected targets selected for analysis as *P. xylostella* was corroborated by comparing their σ_{xx} and σ_{yy} values with the measured values.

Height limitations

The height to which individual targets can be detected by the vertical-looking radar depends on their radar cross-section, which is strongly dependent on their mass. Due to their small size, *P. xylostella* produce signals large enough to be analysed only in the first vertical-looking radar range gate (150–195 m a.g.l.) (Chapman *et al.*, 2002); thus direct observations of *P. xylostella*-sized targets were restricted to targets flying at the altitude covered by this gate. Nevertheless the aerial density–height relationships of other, larger insects were examined in order to establish the flight altitude range of the migrant insect fauna.

Aerial netting

Because the positive identification of targets from their radar signals alone is rarely possible, the insect fauna at the altitude of the lowest gate was sampled, using a balloon-supported net. Air traffic regulations limit the use of high-flying tethered balloons to specially approved areas, so netting was carried out at Cardington Airfield, U.K. (52°06′N, 0°25′W). This is ≈30 km north of the Rothamsted vertical-looking radar, but given the spatially random nature of the overflying populations, as shown by suction trap data (Taylor, 1974), it is assumed that the composition of the catch was reasonably representative of the insect fauna detected by the radar. In July 2000, insects were caught in a tapering net of 0.64 m² aperture, suspended from a tethered, aerodynamically shaped, helium-filled balloon (Reynolds *et al.*, 1999). The net was equipped with a radio-controlled closing device to prevent contamination with low-flying fauna during hauling down. Sampling was carried out between 180 and 200 m a.g.l. Nocturnal samples (≈21.00–03.00 hours) were collected every night from 16 to 24 July, with the exception of 22 and 23 July when netting was impractical due to strong winds.

Deducing P. xylostella *population changes*

The population density of *P. xylostella* in the U.K. in 2000, relative to previous years, was investigated by comparing geometric mean annual catches in Rothamsted Insect Survey light traps from 1980 to 2000. For spring and early summer 2000, temporal patterns of abundance were produced by plotting the geometric mean daily counts of *P. xylostella* from 18 Rothamsted Insect Survey light traps distributed throughout the U.K. (Woiwod & Harrington, 1994). These patterns were compared with equivalent radar records of the nocturnal aerial density of *P. xylostella*-like targets, by correlating the two data sets sequentially with a series of time lags.

Information on the first appearance of adult *P. xylostella* in various northern European countries was obtained from Bülte (2001) (Germany) and from moth migration websites (Belgium: http://users.skynet.be/bs663526/; The Netherlands: http://www-zma.bio.uva.nl/departments/entomol/migrating.html; Finland: http://www.netti.fi/~avanto/havainnot.html).

Meteorological data and flight trajectories

In order to investigate the weather associated with the high-altitude migrations of *P. xylostella*-like targets that were detected on the radar in May, surface and upper air data (temperature, wind speed, direction) were obtained for the nearest sounding stations to the vertical-looking radar site, Hemsby on the east Norfolk coast and Herstmonceux in East Sussex. These data were also collected for two sites located in the area from which it was deduced that the targets had taken off, i.e. Uccle in Belgium and De Bilt in The Netherlands. These data were acquired from a University of Wyoming website (http://weather.uwyo.edu/upperair/sounding.html). The upper air data were used to identify those nights during May 2000 (and a few nights in June) when the *P. xylostella*-type targets detected by the vertical-looking radar at Rothamsted could have used the wind to fly from continental Europe, assuming an 8-h flight endurance. For nights when immigration from continental Europe was considered possible, separate back-tracks were constructed using the 20.00 hours and 04.00 hours weather charts, in order to delineate possible source areas for the immigrants. It was assumed that the winds were geostrophic, i.e. derivable from the pattern of surface isobars (an assumption justified by the slow change in pattern and by the lack of curvature of the isobars during these occasions), and that the insect velocity was the same as that of the wind.

Results

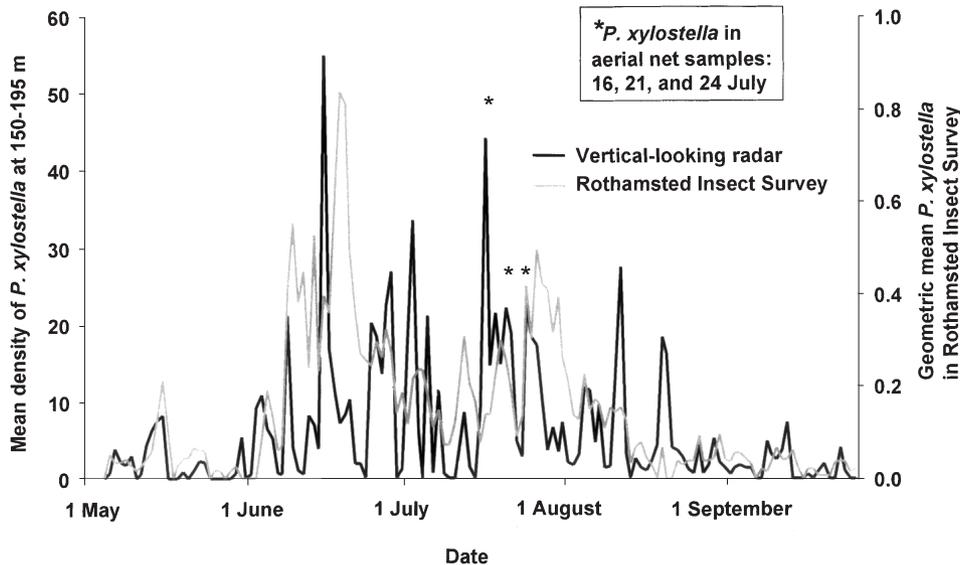### *Annual fluctuations in abundance of* P. xylostella

The geometric mean annual catches in Rothamsted Insect Survey light traps showed that the abundance of *P. xylostella* fluctuated considerably between 1980 and 2000 (Fig. 1), with a maximum in 1996, a year noted for very high migrant activity by many species of Lepidoptera. The year 2000 had the third highest rating of the 21-year period.

Identification of P. xylostella *from vertical-looking radar data*

Targets that fitted the identification criterion (i.e. nocturnal insects weighing between 1 and 4 mg) were detected by the vertical-looking radar in 2000 from early May onwards
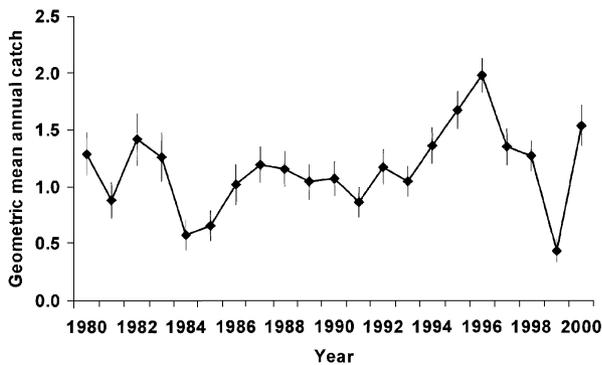
Fig. 1. Geometric mean annual catches (±1 SE) of *Plutella xylostella* in Rothamsted Insect Survey light traps from 1980 to 2000.
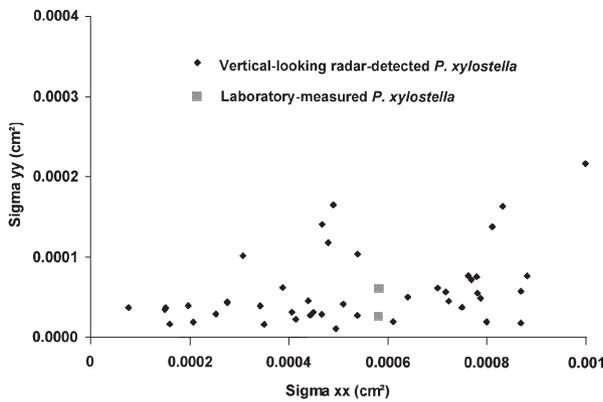
(Fig. 2), which is when this species first appeared in the light traps. Further evidence that these targets were indeed *P. xylostella* was provided by the radar scattering terms. During May, all the radar-detected putative *P. xylostella* had similar values for σ_{xx} and σ_{yy} (Fig. 3), suggesting that the migrants were morphologically similar. Furthermore, the ratios of $(\sigma_{xx}/\sigma_{yy})$ were ≈10:1, indicating that the targets had rather elongated bodies, which would be expected of a delicate microlepidopteran such as *P. xylostella*. Critically, the values of σ_{xx} and σ_{yy} for the radar-detected targets were highly consistent with the laboratory measurements for *P. xylostella* (Fig. 3). The data for the rest of the flight season were similar.

On three nights (16, 21, and 24 July), aerial netting at Cardington yielded single *P. xylostella* at ≈200 m, and these three individuals were the *only* lepidopterans caught during the period of concerted trapping in July. The catching of single specimens may not seem very noteworthy, but experience with this collecting method has indicated that at altitude, the aerial density of Lepidoptera is normally so low that catches of any sort are rather unusual. The clear inference is that a high intensity migration of *P. xylostella* occurred on these nights, a result entirely consistent with the fact that the radar detected high densities of *P. xylostella*-type targets on these and other nights in July (Fig. 2). It is thus concluded that *P. xylostella* was the most common nocturnal species in this mass range flying at ≈200 m a.g.l.

Day-to-day fluctuations in P. xylostella *in May to September 2000*

Plutella xylostella first appeared in the Rothamsted Insect Survey light traps on 5 May, with the first notable

Fig. 2. Mean aerial density of *Plutella xylostella*-type targets (per $10^7 \, m^3$) detected in the first range gate of the vertical-looking radar (150–195 m) above Rothamsted, *P. xylostella* caught in the aerial net at ≈200 m, and geometric mean daily catches of *P. xylostella* in Rothamsted Insect Survey light traps during the whole flight period (May to September 2000).

Fig. 3. Radar scattering terms of laboratory-reared *Plutella xylostella* and vertical-looking radar-detected *P. xylostella*-like targets during the May 2000 immigrations.

peak on 14 and 15 May. Thereafter, catches tended to increase until mid June before starting to decline, albeit with very considerable day-to-day variation (Fig. 2). The aerial density of *P. xylostella*-like vertical-looking radar targets was strikingly similar to the light trap catches, both overall and in terms of day-to-day fluctuations, particularly during May and June (Fig. 2). Correlation analysis over the whole season showed a high degree of similarity between the two ($r = 0.45$) and an even closer relationship over the period 1 May to 30 June ($r = 0.55$).

It seemed very unlikely that the insects seen by the radar to be flying at high altitude would be susceptible to direct sampling by light traps; if they were to be caught at all it would be after descent and landing, and most probably after take-off on the following night. Accordingly, the correlation coefficient was re-computed after introducing time-lags between the light trap and vertical-looking radar data, and it was found that for the May to June period, the best fit was obtained when the vertical-looking radar data were shifted forward by one night ($r = 0.57$). Thus, peaks and troughs in the aerial density of overflying *P. xylostella*-type targets were correlated most highly with catches of *P. xylostella* in light traps for the *following* night. Positive time-lags of more than 1 day, or negative time-lags, produced successively decreasing correlation coefficients.

The height and direction of flight of migrant insect fauna

During the period 5–11 May, the bulk of insect migration occurred within the altitude range of 363–550 m (Fig. 4). Radio soundings of air temperature recorded at Hemsby and Herstmonceux during this period revealed the presence of nocturnal inversions (Fig. 5), with air temperature maxima occurring within the altitude range of 300–400 m a.g.l. Thus, it appears that the migrants were choosing to fly at, or close to, altitudes where the air was warmest. The general direction of movement was towards the west at all altitudes throughout this period.
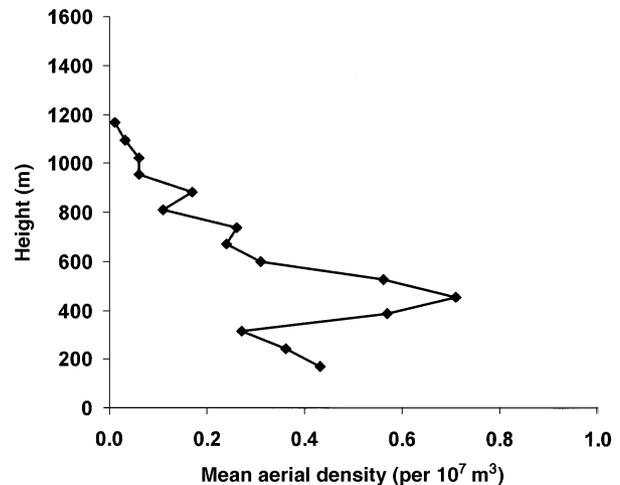

Fig. 4. Density–height profile of larger insects (body mass > 10 mg) detected by the vertical-looking radar in each of the 15 range gates (between 150 and 1166 m) during the first wave of *Plutella xylostella* immigrations (5–11 May 2000).
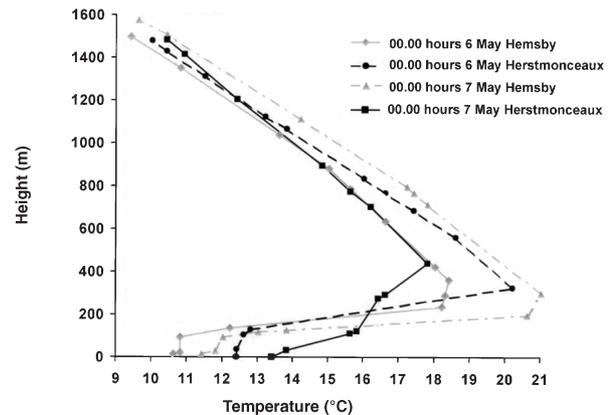

Fig. 5. The variation of air temperature with height at 00.00 hours on the nights of 5/6 and 6/7 May 2000 at Hemsby (Norfolk) and Herstmonceux (East Sussex).

Weather experienced by overflying P. xylostella-*like targets*

Because the main focus of the study was the source of the U.K. population of *P. xylostella* in 2000, the first overflights of the season that occurred from 5 to 15 May (Fig. 6) were studied in detail. The synoptic weather pattern changed little during this period, with stable areas of high pressure over Scotland and Norway, and low pressure over France, which combined to produce persistent, mild winds from the east. The weather was unseasonably warm in continental north-western Europe during this period, with surface temperatures remaining as high as 15–20 °C at 00.00 hours (Fig. 7). Early evening ground temperatures would therefore have been particularly favourable for moth take-off. Night-time surface temperatures at Hemsby and Herstmonceux were not so high, as represented by the 00.00 hours
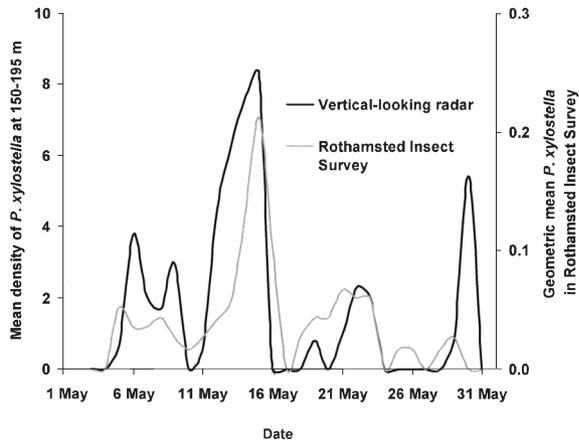
Fig. 6. Mean aerial density of *Plutella xylostella*-type targets (per $10^7 \, m^3$) detected in the first range gate of the vertical-looking radar (150–195 m) above Rothamsted, and geometric mean daily catches of *P. xylostella* in Rothamsted Insect Survey light traps during early season 2000.
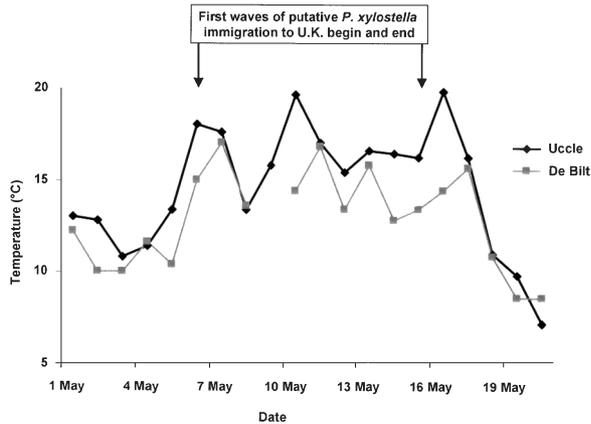

Fig. 7. Midnight surface temperatures (°C) at synoptic meteorological stations in north-western Europe (Uccle, Belgium and De Bilt, The Netherlands) for 1–20 May 2000.

soundings shown in Fig. 5; however there were strong temperature inversions, with maxima of 18–21 °C at heights between 150 and 400 m a.g.l. (Fig. 5). Thus, the *P. xylostella*-like targets detected by the vertical-looking radar between 150 and 195 m would have been flying in exceptionally warm airstreams moving into the U.K. from north-western Europe.

Evidence for continental sources of P. xylostella

In 2000, adult *P. xylostella* first appeared in northern and western Europe from mid April onwards (Finland, 20 April; The Netherlands, 27 April; Belgium, 29 April; Germany, 4 May), so there was clearly a potential source of immigrants
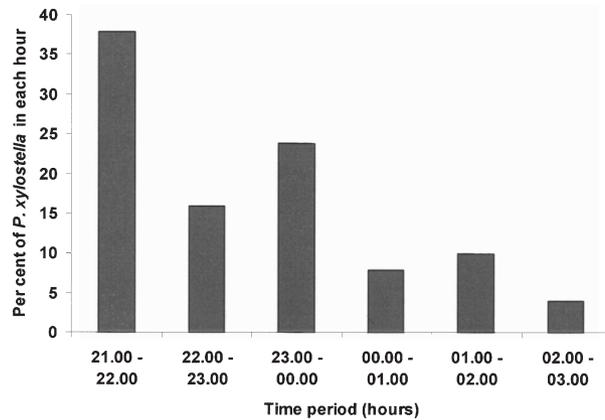
Fig. 8. The percentage of *Plutella xylostella*-type targets detected by the vertical-looking radar in each hourly sample period between 21.00 and 03.00 hours. The data are mean values for the first wave of migrations between 5 and 15 May 2000.

to the U.K. in those areas. Immigration would be possible only if the flight endurance of migrating *P. xylostella* was adequate to allow flight across the North Sea, and no measurements on flight endurance *per se* could be found; however the species is known to be flight active from dusk to dawn (Goodwin & Danthanarayana, 1984; Talekar & Shelton, 1993), and at the time of observations in May, this would indicate an endurance of at least 8 h (20.00–04.00 hours). This deduction was supported by the observation that *P. xylostella*-like targets remained at high altitude throughout the night during the May overflights (Fig. 8).

Inspection of night-time wind vectors at likely flight heights (the top of the temperature inversion, where air temperature was warmest) indicated that North Sea crossings were indeed possible on a number of nights during the period 5–11 May. More specifically, back-tracks constructed for these occasions showed that moths flying over the Rothamsted vertical-looking radar at 04.00 hours, which had taken off at dusk, came from the adjacent continent ≈340–500 km to the east or ENE (Fig. 9a). The estimated source regions of the migrants were central Netherlands on 5 May, southern Netherlands on 6 May, and north-western Netherlands on 10 and 11 May (Fig. 9a).

The wind direction veered to southerly on 14 and 15 May, and back-tracks indicated that the overflights detected at Rothamsted probably came from no further afield than the south coast of England on these nights (Fig. 9b). Similarly, there was no evidence that immigration accounted for overflights in June and July, except on 8 June, when back-tracking indicated possible sources in northern France (Fig. 9c).

Discussion

Investigations of the migration of moths generally rely on indirect evidence derived from light trap catches, with all the uncertainties that this involves. For example, trap
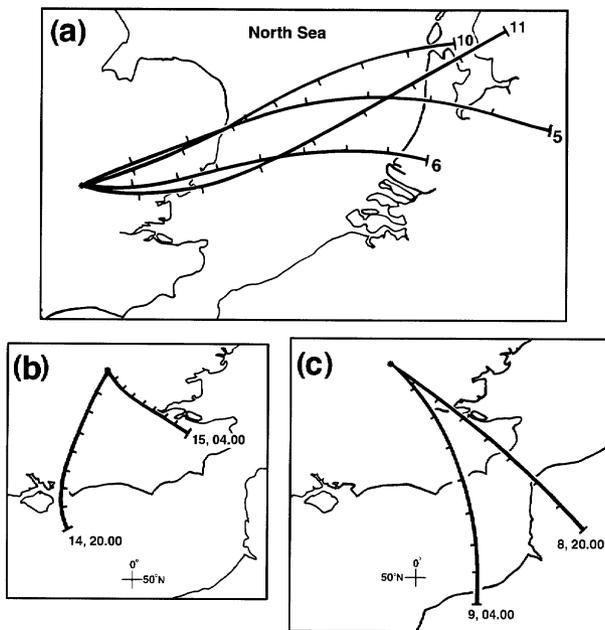
Fig. 9. Back-tracks for *Plutella xylostella*-type targets detected flying over the Rothamsted vertical-looking radar. (a) Back-tracks for the nights of 5, 6, 10, and 11 May 2000, based on the 20.00 hours weather charts and indicating immigration from The Netherlands. (b) Back-track for the night of 14 May 2000, based on the 20.00 and 04.00 hours weather charts and indicating overflights from south-eastern England. (c) Back-track for the night of 8 June 2000, based on the 20.00 and 04.00 hours weather charts and indicating possible immigration from northern France.

catches are influenced strongly by local weather and the lunar cycle (Dent & Pawar, 1988; Yela & Holyoak, 1997). There may also be a time lag of days between an immigration and its manifestation as a peak in nightly catches (Wada *et al.*, 1987), making it difficult to identify the meteorological conditions concurrent with the migration event. Moreover, light traps give no indication of the height of flight of the migrants, which is vitally important for constructing back-tracks because wind speed and direction vary with height. In the case of previous *P. xylostella* studies, the best that could be done was to assume that the species migrates principally at high altitude (Shaw & Hurst, 1969). All these uncertainties can be resolved for unusual and spectacular mass migrations when the evidence about population movement and source areas is overwhelming and unambiguous, but this is rarely the case for more routine movements. In these instances, direct observation of migration as it occurs would be of great supplementary value, and it is precisely this information, available from vertical-looking radar, that has been exploited in this study.

The identification of P. xylostella *by the radar*

The radar targets that were selected for study all had estimated masses within the 1–4 mg range known to be

occupied by *P. xylostella*, and also had σ_{xx} and σ_{yy} values highly consistent with this species. While these data showed that the targets were probably *P. xylostella*, they may have been morphologically similar species of microlepidoptera or other similar taxa; however two other pieces of circumstantial evidence were available. Firstly, *P. xylostella* was the only lepidopteran caught in the aerial net and was the commonest species in the 1–4 mg mass range. Secondly, the day-to-day abundance of *P. xylostella*-like radar targets correlated strongly with Rothamsted Insect Survey catches of this species, especially during the May to June period of interest in this study. The improvement in correlation when the trap catches were lagged by 1 day relative to vertical-looking radar data indicates that the high-altitude migratory flights preceded catches in light traps, and there are sound theoretical reasons to expect this pattern. Adult *P. xylostella* emerge from pupae in the daytime and become active at dusk of the same day (Pivnick *et al.*, 1990); however they do not become sexually mature and reproductively active until 3 or 4 nights post-emergence (Pivnick *et al.*, 1990). This delay in sexual maturation provides a window for migration, and it seems highly likely that *P. xylostella* exhibits the *oogenesis–flight syndrome* (Johnson, 1969). Migrants, particularly those flying at high altitude, are unlikely to be caught by light traps. It is only after their migratory phase is over that they begin to respond to vegetative stimuli (mates, food plants, etc.) by engaging in low-altitude local movements (Kennedy, 1986), and it is during this period that they are likely to be caught in light traps. Overall, the weight of the evidence thus suggests strongly that the selected radar targets actually were *P. xylostella*.

The preferred height of flight of P. xylostella

The results showed that the larger insect fauna (>10 mg) tended to migrate at altitudes of 300–500 m a.g.l. (Fig. 4) in the warm air near the top of the nocturnal temperature inversion (Fig. 5). The concentration of insects in discrete layers at altitudes of several hundred metres has often been detected by radar, both in the U.K. (Smith *et al.*, 2000; Chapman *et al.*, 2002) and elsewhere (Drake, 1985; Drake & Farrow, 1988; Riley *et al.*, 1995), and appears to be a very common feature of long-range migration. The mechanisms by which migrants select and maintain their preferred altitudes are unclear but it is very probable that nocturnally migrating moths would accumulate at heights where the air temperature maximised their flight efficiency. In the case of *P. xylostella*, the optimum temperature for flight activity is 23 °C (Shirai, 1991), and in the present study, the air temperatures closest to this could be found at the top of the temperature inversions (Fig. 5). It thus seems probable that the bulk of *P. xylostella* migration would have occurred above the altitude range (150–195 m) at which targets of this size could be detected.

Flight near the top of a temperature inversion offers benefits other than optimal temperatures for flight; there

is often a maximum in the wind speed in this zone, and any insects flying in it would therefore maximise their migratory range.

The case for immigration

In the period 5–11 May 2000, the winds over the North Sea were such that insects flying at altitudes above 100 m and for ≥ 8 h could certainly have migrated into the U.K. from north-western continental Europe. More specifically, back-tracks of the *P. xylostella*-like targets detected over-flying the Rothamsted radar late in the night suggested that these insects had taken off in The Netherlands, where *P. xylostella* was known to have been present since 27 April. There is thus very strong evidence that this species was immigrating into the U.K. from the beginning of May.

Although *P. xylostella*-sized targets are only detectable in the lowest range gate (150–195 m), it seems highly probable that, like the other migrants detected on the radar, they were flying over an altitude range of at least 300 m. If so, then on the nights of 12–15 May when the average aerial density of *P. xylostella*-sized targets was about four per $10^7 \, \text{m}^3$ at the measurement height, the area density of migrating moths would have been $> 300 \times 10^6 \times 4 \times 10^{-7} = 120$ moths per hectare. An alternative measure of the magnitude of migration is the flux of insects crossing a line perpendicular to the direction of movement. Typically, three or four *P. xylostella*-sized targets intercepted the 8 m wide, 45 m high range gate per night, so on the conservative assumption that the moths were distributed evenly over an altitude range of 300 m, 18–24 individuals passed over the radar per night. This is equivalent to ≈ 3000 westwards-moving migrants per kilometre per night. If, as seems likely, the migration front extended over several hundred kilometres, nightly influxes into the U.K. of several hundred thousand moths would have been occurring. These figures seriously underestimate the magnitude of migration if the *P. xylostella*-like targets were not distributed evenly in altitude but were actually much more dense in regions close to the top of the temperature inversions.

Immigration of *P. xylostella* into the U.K. during 2000 would seem to be a logical extension of a general migration of this species that was taking place within northern Europe in that year. Almost unprecedented numbers reached the Svalbard archipelago, ≈ 800 km north of mainland Scandinavia in the High Arctic, during 2000 (Coulson *et al.*, in press), where it is not resident (Coulson, 2000). Back-tracks showed that the proximate source for most U.K. immigrants was probably The Netherlands and neighbouring countries, such as Belgium and Germany. It is just conceivable that this region might also have been the ultimate source, as *P. xylostella* may have survived in small numbers in Germany in recent mild winters (R. Bülte, pers. comm.), but estimates of the scale of influx into the U.K. make this unlikely. More probably, any putative overwintering populations in northern Europe would have been augmented by migrants from elsewhere. One possibility is that these migrants came from Finland (first record 20 April), as they did during previous mass influxes (French & White, 1960; Shaw & Hurst, 1969), and passed through the Low Countries on route to the U.K. Even so, the Finnish moths must have originated from further south, most probably from the steppes of southern Russia (K. Mikkola, pers. comm.). A much more plausible explanation for the U.K. immigration is that it arose from *P. xylostella* populations overwintering in southern Europe, perhaps in the Mediterranean region, a total journey of ≈ 1500 km. This distance is quite possible if migrants were flying 400–500 km per night (as suggested strongly by the observations), and migrated on three or four successive nights.

The case for overwintering

The major outbreaks of *P. xylostella* in the U.K. in recent years have been shown to be attributable to mass influxes from northern continental Europe (French & White, 1960; Johnson, 1969; Shaw & Hurst, 1969); however it has remained unclear whether the much smaller populations observed in the U.K. in most other years also result from immigration or whether they arise from a residue of overwintering individuals. Much of this uncertainty stems from the fact that it is not known whether the species can survive U.K. winters *in situ*. Some authors have conjectured that it can overwinter (Marsh, 1917; Hardy, 1938), while others doubt that it has the ability to hibernate or diapause at any stage of its life cycle (Talekar & Shelton, 1993). The issue of survival during winter is obviously not restricted to the U.K., but applies to many other temperate areas (some of which have pest problems of much greater severity than the U.K.), and it has important consequences for *P. xylostella* management strategies. For example, the ability to overwinter locally may result in greater persistence of insecticide-resistant populations and, conversely, of their parasitoids. As a result, experimental overwintering studies of all developmental stages of *P. xylostella* in field cages have been undertaken recently in eastern England. These experiments have consistently shown very little survival (R. Collier, pers. comm.), and give no reason to suppose that overwintering occurs to any significant degree.

The implications of the findings

The radar data and Rothamsted Insect Survey catches provided persuasive evidence that hundreds of thousands of *P. xylostella* immigrated into the U.K. in May 2000, and that they probably came from southern or south-eastern Europe. This immigration is in contrast to the well-studied mass invasions of the 1960s, which arrived much later in the season from large, well-established Scandinavian populations (French & White, 1960). While it is possible that further immigrations took place later in 2000 (e.g. 8 June; Fig. 9c), most of the high-altitude migratory flights detected by the radar from June onwards suggested a within-U.K.

redistribution of locally emerged moths of the second and third generations.

The magnitude of the immigration, and the absence of evidence to support the overwintering hypothesis, identify long-distance migration from continental Europe as the key factor in the establishment of U.K. populations. While this scenario has been accepted tacitly as the likely origin of *P. xylostella* in the U.K., this study is the first to demonstrate it by direct observation, and in a year when populations did not reach epidemic proportions. Moreover, the study indicates that early-season immigration of moths from southern Europe accounted for the U.K. population, rather than late-season mass migration of well-established populations from the Baltic region.

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