

Title: Mass seasonal bioflows of high-flying insect migrants

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Abstract: Migrating animals impact ecosystems directly via influxes of predators, prey and competitors, and indirectly by vectoring nutrients, energy and pathogens. While linkages between vertebrate movements and ecosystem processes have been established, the effects of mass insect ‘bioflows’ are undescribed. We quantified biomass flux over southern UK for high-flying (>150 m) insects, and show that ~3.5 trillion insects (3200 tons of biomass) migrate above the region annually. These flows are not randomly directed in insects larger than 10 mg, which exploit seasonally-beneficial tailwinds. Large seasonal differences in the southward versus northward transfer of biomass occur in some years, although flows were balanced over the 10-year period. Our long-term study reveals a major transport process with implications for ecosystem services, processes and biogeochemistry.

One Sentence Summary: Enormous long-distance atmospheric transport of insect biomass occurs in seasonally-predictable directions

Main Text: Latitudinal migrations of vast numbers of flying insects, birds and bats (1–7) lead to huge seasonal exchanges of biomass and nutrients across the Earth’s surface (8–11). Because many migrant species (particularly insects) are extremely abundant (1, 5), seasonal migrations may profoundly affect communities through predation and competition while transferring enormous quantities of energy, nutrients, propagules, pathogens and parasites between regions, with substantial effects upon essential ecosystem services, processes and biogeochemistry (8–11), and ultimately ecosystem function.

Latitudinal bird migrations are well characterized; e.g. 2.1 billion passerines migrate annually between Europe and Africa (2), integrating multi-sensory navigational information (12), exploiting favorable winds and adopting adaptive flight behaviors (13). By comparison, even though insect migration surpasses all other aerial migratory phenomena in terms of sheer abundance (1), latitudinal insect migration is largely unquantified, in particular for the majority of species that migrate hundreds of meters above the ground (5). Specialized radar techniques are required to study these high-flying insect migrants as they are too small to carry transmitters or be observed by any other means (14). Until now, radar studies have been aimed almost exclusively at quantifying migrations of relatively few nocturnal species of agricultural pests (3), and no study has yet quantified the hugely abundant and ecologically-important daytime insect migrants.

We quantified annual abundance and biomass of three size categories of diurnal and nocturnal insects migrating above an area of ~70,000 km² of the southern UK (Fig. 1A), between 150–1200 m above ground level (agl) (Fig. 1B), from 2000–2009 (15). Abundance and biomass values for medium (10–70 mg) and large insects (70–500 mg) (referred to collectively as ‘larger insects’) were calculated from measurements of >1.8 million individuals (table S1) detected by Vertical-Looking entomological Radars (VLRs) located in southern UK (Fig. 1A). The VLRs provide a range of information – including body mass, flight altitude, aerial density, displacement speed, displacement direction, and flight heading – for all individual insects of >10 mg body mass that fly through the vertically-pointing beam within the altitude range of 150–1200 m agl (14). Annual

abundance and biomass values for larger insects migrating over the study area were extrapolated from the aerial densities and body masses recorded above the VLR locations (15). The third size category, small insects (<10 mg), are not sampled by VLRs, and so abundance and biomass data were calculated from aerial netting samples (16) taken ~200 m agl near one of the radars (Fig. 1A) and extrapolated to the study area (15). Larger diurnal migrants are predominantly beneficial species, including hoverflies, ladybeetles, carabid beetles, and butterflies (14–17), and the most abundant small day-fliers are cereal aphids (16). The commonest larger nocturnal insects are lacewings and noctuid moths (14, 16), while Diptera comprise the majority of the small nocturnal insects (16).

An annual mean of 3.37 trillion insects (range: 1.92–5.01 x 10¹²; Fig. 1C and table S2) migrated high above the study region, comprising 3200 tons of biomass (fig. S1 and table S3), of which >70% occurred during daytime (Fig. 1C and table S2). Numerically, >99% of individuals were small insects, yet while the 15 billion medium and 1.5 billion large insects comprised only 0.4% and 0.05% of the annual abundance (table S2), they accounted for a substantial proportion of the biomass: 12% (380 tons) and 7% (225 tons) respectively (table S3).

By analyzing 1,320 daytime ‘mass migrations’ (15) involving 1.25 million VLR-detected insects, and 898 nocturnal mass migrations involving 126,000 insects (table S1), we characterized migration directions of the larger insects during ‘spring’ (May–June), ‘summer’ (July) and ‘fall’ (August–September) (fig. S2 and table S4). Although high-altitude winds blew consistently towards the north-east/east in all three seasons (Rayleigh tests; daytime: spring, 60°; summer, 66°; fall, 84°; night-time: spring, 69°; summer, 81°; fall, 101°; Fig. 2A and table S5), mass migrations of larger insects did not simply move with the prevailing south-westerly winds. During the spring, mass migrations were consistently towards the north (Rayleigh tests; daytime: medium, 333°; large, 329°; night-time: medium, 349°; large, 349°; Fig. 2A), indicating that migration occurred on winds with a significantly more southerly component than prevailing winds (Watson-Wheeler tests; $P < 0.0001$ in all cases; table S5). Summer mass migrations were randomly directed (Rayleigh tests; P

> 0.05 in all cases; Fig. 2A and table S5), indicating an absence of wind selectivity. By contrast, fall mass migrations were consistently directed towards the south (Rayleigh tests; daytime: medium, 174°; large, 159°; night-time: medium, 181°; large, 180°; Fig. 2A), indicating active selection of winds with a significantly more northerly component than the prevailing winds (Watson-Wheeler tests; $P < 0.0001$ in all cases; table S5). These relationships indicate preferred movement directions during the spring and fall, and selection of days and nights with favorably-directed tailwinds. Seasonally-beneficial migration directions have been previously reported in a few species of large insects, notably pest noctuid moths (3, 14, 18), but our findings demonstrate the ubiquity of such movements among a diverse array of insect migrants for the first time. Since small insects fall below the VLR's detection threshold (14) and thus their tracks cannot be directly measured, we used aphid migration intensity as representative of all small insect migration (fig. S3) by analyzing wind directions associated with mass migrations of aphids (15). We found that aphid migration directions closely match prevailing wind directions, i.e. towards the north-east in all seasons (fig. S4), and therefore conclude that these small insects do not have mechanisms for selecting seasonally-beneficial winds.

The greatest amount of variation in the aerial density of diurnal migrants was explained by surface meteorological conditions associated with fine weather (table S6): migration intensity was greatest on warm days (fig. S5A), with moderate to high surface heat flux (fig. S5B), and low surface wind speeds (fig. S5C). However, the strong relationship with fine weather does not explain the directed movements of the larger insects in spring and fall. Models indicated that during these seasons (but not summer), surface wind direction was also correlated with migration intensity, with high densities associated with southerly winds in the spring and northerly winds in the fall (table S6). Surface and high-altitude daytime wind directions were strongly correlated in all seasons (tests for T-linear association; $P < 0.001$ in all cases; fig. S6), but not at night (18). Thus surface wind direction provides a reliable cue regarding the suitability of winds aloft for diurnal migrants at take-off, but not for nocturnal migrants which must employ other methods for assessing high-altitude

wind direction (19). The ubiquity of tailwind selectivity in such a diverse group indicates that compass mechanisms must be universal in larger insect migrants.

If high-flying insects have a compass sense, one would predict that in addition to selecting a favorable tailwind, they would also orientate in the seasonally-beneficial direction, and thus actively contribute to their wind-assisted displacement. Such “common orientation” was indeed highly prevalent in the larger insects (table S1), and headings were close to tracks (fig. S7): northwards in the spring and southwards in the fall (table S7). The close correspondence between headings and tracks signifies that larger insects added much of their self-powered airspeed to the wind vector, and thus achieved rapid displacement speeds [10–16 m/s (36–58 km/h); Fig. 2B; table S7]. A flight duration of 4 hours could therefore result in transport over >200 km, and during spring and fall this transfer of biomass and nutrients occurs in predictable directions.

What are the implications of this high-altitude insect movement? Insect bodies are typically comprised of 10% nitrogen and 1% phosphorus by dry weight (20), and as such they represent a rich source of nutrients which can be limiting for plant productivity (11). The 3200 tons of biomass moving annually above our study region contains ~100,000 kg of N and 10,000 kg of P, representing 0.2% of the surface deposits of N and 0.6–4.7% of P from the atmosphere, comprising 5.78×10^{12} Joules of energy (15). To put these seasonal movements in context, the annual airborne insect biomass >150 m above the southern UK is 4.5 times greater than the 2.2 billion (700 tons) of bogong moths (*Agrotis infusa*) which migrate to the Australian Alps every summer (7, 9), 7.7 times greater than the 30 million songbird migrants (415 tons) which depart the UK for Africa each fall (table S8), and >40 times greater than the 150 million monarch butterflies (75 tons) which migrate between Eastern North America and Mexico (14).

If the spring and fall movements documented here perfectly counter-balance each other there would be no net annual exchange of energy and nutrients, and the principal consequences would be the exchange of genes, pathogens and parasites. Over the 10-year study we found that net northward spring movements of larger insects were almost exactly cancelled out by net southward

fall movements; however, on an annual basis the net flux could be up to 200 tons greater in either direction (Fig. 3). Such insect movements represent an underappreciated mechanism for redistributing nutrients and energy, and if the densities observed over southern UK are extrapolated to the airspace above all continental landmasses, high-altitude diurnal insect migration represents the most important annual animal movement in terrestrial ecosystems, comparable to the most significant oceanic migrations (21). Given the worrying declines in many migrants (8), developing global surveillance techniques (6) for long-term observation and prediction of the impacts of mass aerial migrations at such macrosystem scales (22) should be a priority for ecologists.

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Supplementary Materials:

Materials and Methods

Figures S1-S8

Tables S1-S8

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Figure Legends

Fig. 1. Monitoring migration intensity above the southern United Kingdom. (A) The intensity and direction of high-altitude insect migration through the atmosphere 150–1200 m above ground level (agl) was measured over a 70,000 km² region of the southern UK (black circle) under continual surveillance from vertical-looking radars (VLR, left inset) at 3 locations (white dots); the aerial insect fauna was sampled by balloon-supported aerial netting at 200 m agl (center-right inset) and 12-m high suction traps (bottom-right inset). (B) Vertical profiles of larger insect (>10 mg) migration intensity over the sampling range of the VLRS. (C) Annual totals of insects migrating above the study region, during daytime, dusk, and night, and combined for the whole 24 hours. Lines represent annual totals; in the box plots, the central bar represents the median, boxes represent the interquartile range (IQR), whiskers extend to observations within ± 1.5 times the IQR and dots represent outliers.

Fig. 2. Migratory directions and speeds of high-flying larger insects. (A) Despite prevailing winds blowing towards the northeast in all seasons, migratory tracks and headings occurred predominantly in seasonally-beneficial directions in spring and fall, but were randomly directed in summer. Small black circles on the periphery of the circular histograms represent mean directions of individual mass migrations, and the color bar indicates the percentage of migrations in each 22.5° bin. The bearing of the blue arrow indicates the overall mean direction, and arrow length represents the circular resultant length (r). (B) Migrants achieved fast displacement speeds. Solid black bars represent medians, dashed red lines represent means, boxes represent the IQR, whiskers extend to observations within ± 1.5 times the IQR, and dots represent outliers.

Fig. 3. Annual patterns of net directional migration. The net flow of biomass of larger insects above the study region, in spring (blue), fall (red), and the whole year (black). Negative values indicate a net southward movement, while positive values indicate a net northward movement. In the box plots, central bars represent median values, boxes represent the IQR, whiskers extend to observations within ± 1.5 times the IQR, and dots represent outliers.

Fig 1

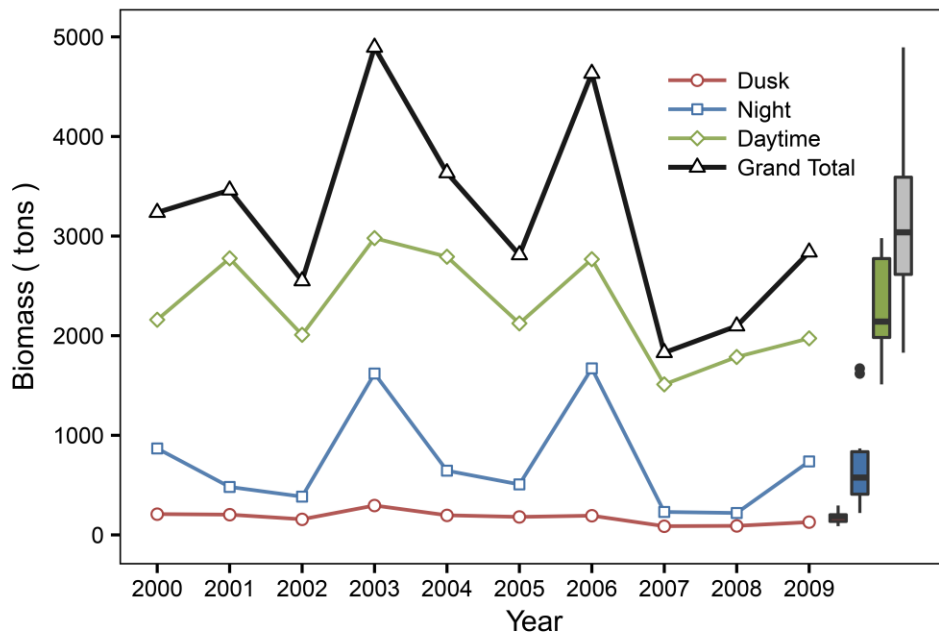
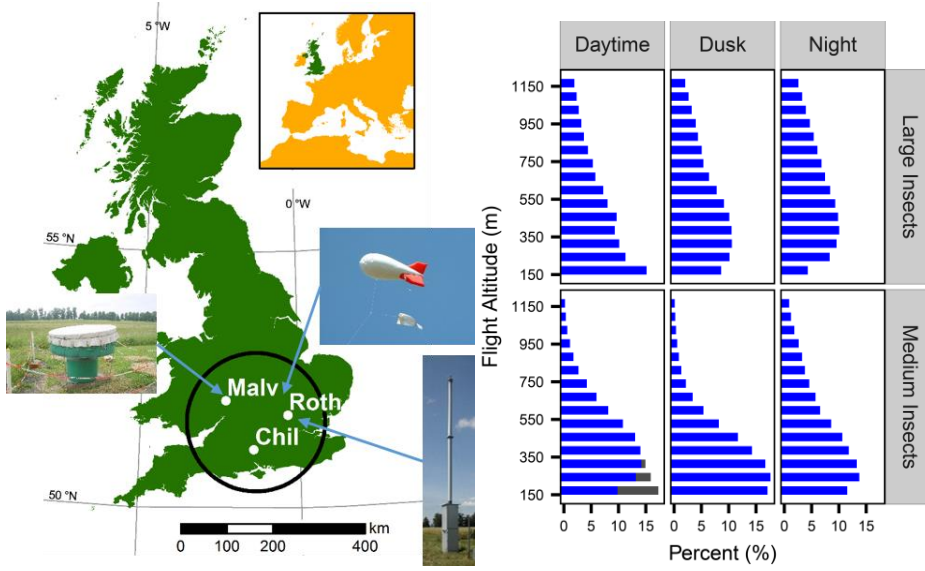


Fig 2

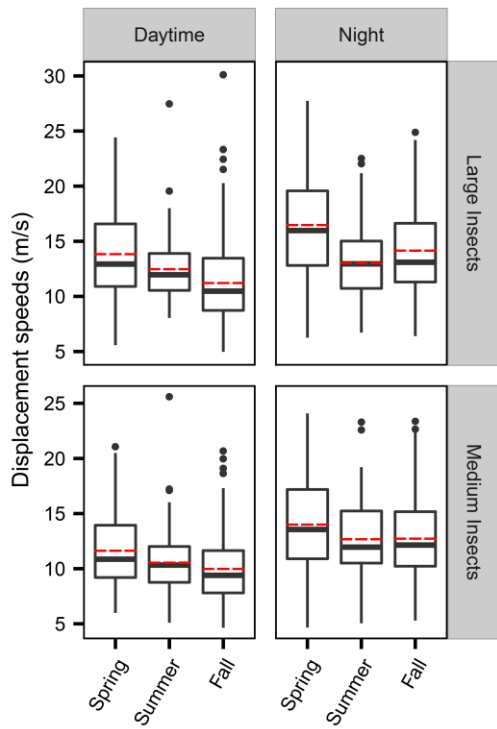
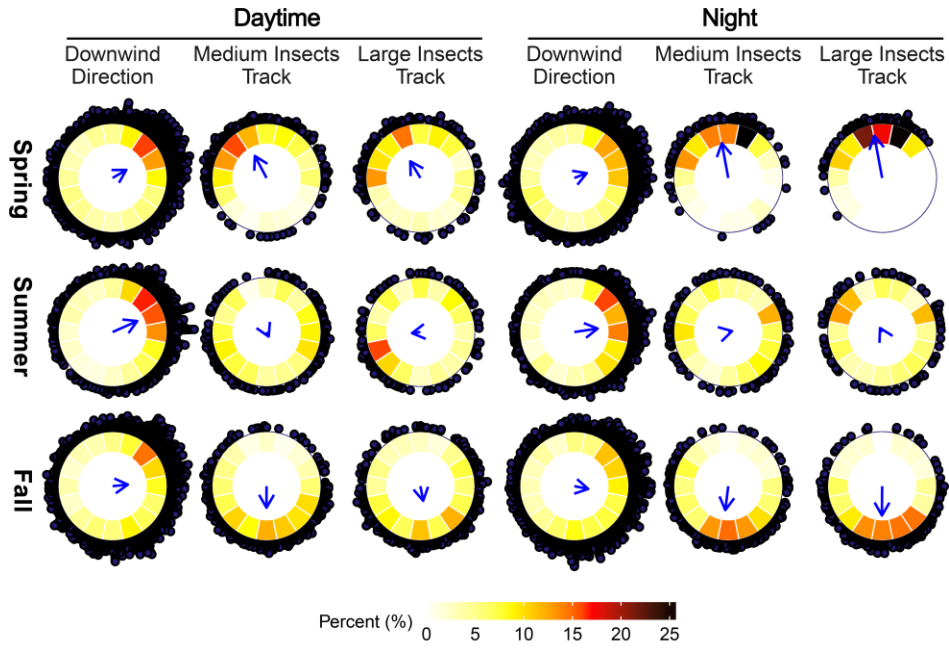
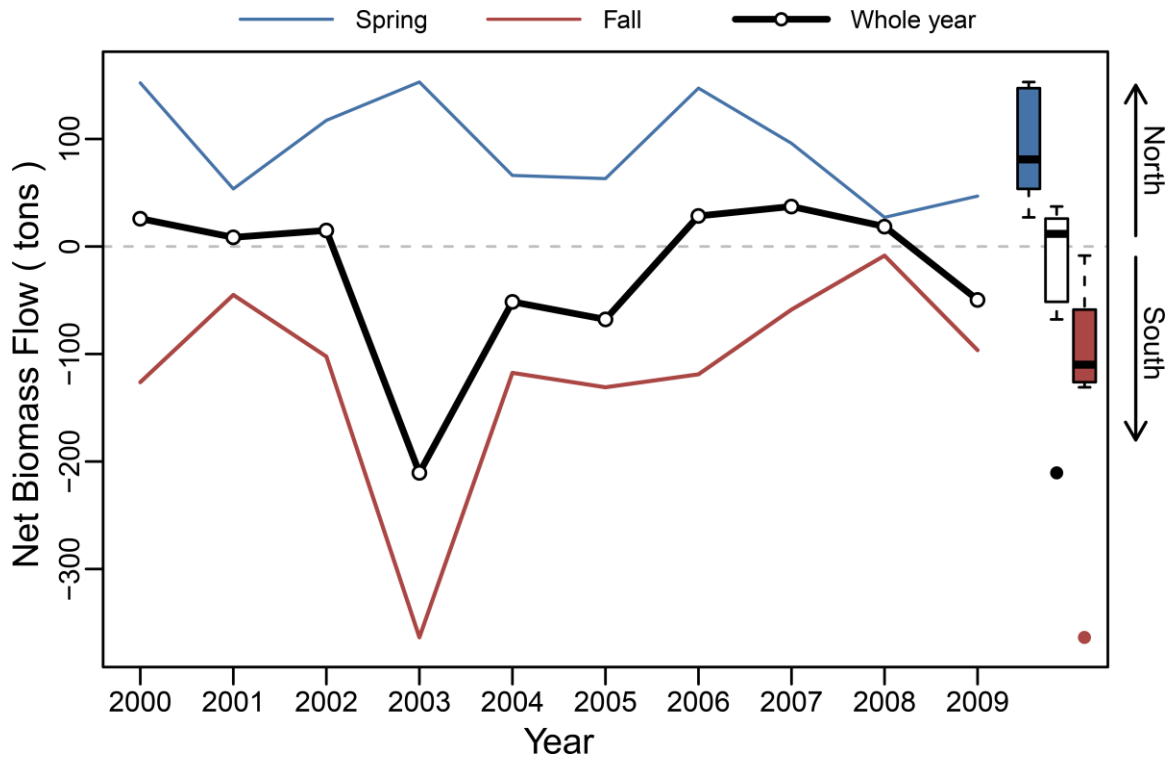


Fig 3





Supplementary Materials for

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Materials and Methods

Radar observations of high-altitude migrations of larger insects (10 – 500 mg)

We measured the migration intensity of high-flying (>150 m above the ground) ‘larger’ insects (with body masses between 10 and 500 mg) during daytime, dusk and night-time periods of the spring, summer and fall of the 10-year period from 2000 until 2009 inclusive, using data collected by purpose-built, vertical-looking entomological radars (VLRs) situated in southern England. The VLR equipment and operating procedures are described in detail elsewhere (14, 23). Briefly, the radars provide a range of information – including body mass, flight altitude (insects are detected within 15 separate altitude bands), aerial density, displacement speed, displacement direction, and flight heading – for all individual insects of >2 mg body mass that fly through the vertically-pointing 3.2 cm wavelength (X-band) beam within the altitude range of 150–1200 m agl. The VLRs are operated for a 5-minute sampling period every 15 minutes throughout the 24-h daily cycle, thus giving a total of 96 sample periods within each 24-hour period. Due to multiple-target interference (see below), small insects (those with body masses <10 mg) are not sampled effectively by VLRs, and so we restricted the radar analyses to insects we defined as ‘larger insects’ which had body masses >10 mg up to a maximum of 500 mg. Migratory insects with body masses >500 mg are extremely rare in the UK, and so we excluded the few, possibly anomalous, radar targets above this size. Migration intensities of small insects (those with body masses <10 mg) were calculated from aerial sampling (see below).

The ‘larger’ insects detected by VLRs were further divided into two size categories, which we defined as ‘medium’ insects (with body masses from 10 mg to 70 mg), and ‘large’ insects (with body masses from 70 mg to 500 mg). Extensive aerial netting samples collected at heights of around 200 m above the ground during the spring, summer and fall periods of the years 1999 to 2007 were taken at a site in central Bedfordshire (Cardington airfield) which was just 35 km to the north of the Rothamsted VLR (16). Examination of these aerial samples of thousands of high-flying insects above the UK indicated that the most abundant dayflying migrants in the medium size category were hoverflies (Diptera: Syrphidae), carabid beetles (Coleoptera: Carabidae), and ladybird beetles (Coleoptera: Coccinellidae) (16, 24, 25). The large dayflying category probably mostly comprised migrant butterflies (Lepidoptera) (17) and perhaps some dragonflies or damselflies (Odonata) (26). During dusk and night-time, aerial samples indicate that the most abundant medium-sized insects are green lacewings (Neuroptera: Chrysopidae) and large flies (e.g. Diptera: Tipulidae) (16, 27), and the large size category are predominantly large noctuid moths such as *Autographa gamma* and *Noctua pronuba* (Lepidoptera: Noctuidae) (3, 16).

Because the VLRs document the total migration intensity of insects of different body masses throughout the sensed volume of the atmosphere above the radar, and this sensed volume is precisely known for all possible insect body masses (28), we were able to accurately quantify the total migration intensity through the study region (in terms of numbers of individuals) and the total biomass of this population (see below for description of the methods). Radar data on the migration intensity of larger insects was collected throughout the entire 24-hour period of each day, and separate values were calculated for three time-periods: ‘daytime’ was defined as the period from 1 hour after sunrise until 1 hour before sunset; the ‘dusk’ period was defined as 1 hour before sunset until 1 hour after sunset; and the ‘night-time’ period was defined as 1 hour after sunset until 1 hour before sunrise the following morning (29). Data

were collected throughout the vertical sampling range of the VLRs, that is at heights between 150 m and 1200 m, and from above the following VLR locations: Malvern, Worcestershire (lat. 52° 06' 04" N, long. 2° 18' 38" W) in south-western England from 2000 to 2003; Chilbolton, Hampshire (lat. 51° 8' 40" N, long. 1° 26' 13" W) in south-central England from 2004 to 2009; and Rothamsted, Harpenden, Hertfordshire (lat. 51° 48' 32" N, long. 0° 21' 27" W) in south-eastern England from 2000 to 2009.

In order to define the spring, summer and fall periods, we plotted migratory track directions of the larger (VLR-detected) insects on a monthly basis (fig. S2, table S4). There was a clear seasonal pattern during both the day and night, with seasonally-beneficial movements towards the north in May and June, followed by a period of randomly-directed movements in July, and then seasonally-beneficial movements once again in August and September but this time directed southwards (fig. S2, table S4). Radar data for the months preceding and following the May–September migration period were far too sparse for analysis, and so were excluded from further analysis. We therefore defined the spring migration period as May and June, the mid-summer period as July, and the fall migration period as August and September, similar to the observed pattern of seasonal movement directions in previous analyses of high-altitude insect migration (30, 31).

The three radar locations are approximately 100–120 km apart, and preliminary observation of the data in the current study, and previous analyses of nocturnal data (3, 4, 18, 31), indicate that the aerial densities, migration directions, movement speeds, flight altitudes and taxonomic diversity measured at each site were very similar. We therefore combined our data from the 3 radar locations for the purposes of analysis, and we assumed that the data collected at each location was representative over distances of up to at least 120 km away from each site. We defined our study region as the volume of atmosphere between 150–1200 m above ground level (agl), above an area delimited by a circle of 300 km diameter (see Fig. 1A in main paper), which had a surface area of 70,686 km². The height range of 150–1200 m was primarily selected as this is the sampling range of the VLRs and we therefore have the most reliable data from this height range. In the UK, there will be extremely limited migration above the 1200 m ceiling as it is generally too cold above this height for insect flight (14), and examination of the VLR-measured vertical profiles of insect density (see Fig. 1B in the main paper) indicates that densities decline with increasing altitude to very low values in the highest sampling band of the VLR just below 1200 m. We therefore conclude that insect migration intensities above our 1200 m ceiling are negligible. Below 150 m, insect densities will be much higher (for example, at 12 m they are approximately ten times greater than at 200 m; see fig. S3A); however, these lower-flying insects will not be involved in the long-range seasonal movements we are concerned with in this paper, and therefore we excluded them from our analyses. Our reasoning for this is that even very small and weak-flying insect migrants (such as aphids) have vertical ascent rates of between 0.14 – 0.25 m/s (32), while larger insect migrants can climb at speeds of 0.5–2.5 m/s (14); thus even the slowest-climbing migratory insects will rise above 100 m in about 10 minutes of flight. Given that we are concerned with long-range exchanges of insect biomass and nutrients in this study, we therefore decided to exclude all aerial insect densities below the VLR lowest sampling height of 150 m agl, as the short flights which occur at low altitudes will be unimportant in terms of seasonal long-range transport.

A “migration occasion” was defined as any occasion when at least 1 larger insect (i.e. 1 medium-sized or 1 large insect) was detected in the daytime or night-time periods by one of the radars between 150–1200 m agl; this resulted in 5,308 occasions (containing 1.667 million individual radar-detected insects)

being available for analysis during the day, and 4,876 occasions (containing 168,000 individual insects) during the night (table S1). This dataset was used to calculate the seasonal and annual patterns of migration intensity and biomass of the larger insects (see below). To analyze directional patterns (see below), we used a subset of the data which we termed ‘mass migrations’; these were defined as the cumulative migration occasions which accounted for 75% of the total number of individual insects in each season / size category combination. This resulted in 1,320 of the daytime occasions (25% of the total occasions, involving 1.248 million individual insects), and 898 of the night-time occasions (18% of the total occasions, involving 126,000 insects), being defined as mass migrations (table S1).

Calculation of high-altitude migration intensity and biomass of larger insects (10–500 mg)

Migration intensities of high-flying (>150 m agl) larger insects (with body masses >10 mg) are effectively monitored with the VLRs. We calculated an aerial density value (per 10^7 m³) for each individual larger insect detected by the radars during the study period (daytime, dusk and night-time periods of the spring, summer and fall of each year during 2000–2009), based upon the volume of atmosphere sensed by the VLR and the displacement speed of each individual insect (28). The total aerial density of migrating larger insects above each radar site during each of the diel time periods during the spring, summer and fall migration seasons in each of the 10 years was calculated in the following manner. Firstly, we calculated the aerial density of the total medium and total large insects detected in each of the VLR’s 15 altitude bands in the daytime, dusk and night-time periods, and plotted the mean values in each altitude band over the study period (the blue bars in Fig. 1B of the main paper). The lowest altitude bands showed reduced densities of the highly-abundant medium insects during the daytime (bottom-left panel of Fig. 1B), due to high levels of multiple-target interference caused by two or more insects passing through the beam in the same altitude band and at the same time (14), a phenomenon routinely experienced in the lowest gates during intense daytime migrations (28, 29). We corrected for this underestimation of true aerial densities in the first three altitude bands by fitting a log-linear regression to the observed aerial density values of medium dayflying insects in altitude bands 15 down to 4, and then extrapolating this to produce expected aerial densities in altitude bands 1 to 3 (fig. S8a). This produced estimated aerial densities that were 1.761, 1.208 and 1.054 times the observed values in altitude bands 1, 2 and 3 respectively (fig. S8a). These corrected values were used to plot the density-height relationship of the dayflying medium insects, and the additional density that was added by this process is shown by the black component of the horizontal bars in Fig. 1B of the main paper. The only other size class / time period combination with substantially lower densities in the lower altitude bands was for the large night-flying insects, but this is a genuine phenomenon (i.e. not caused by multiple-target interference) caused by congregation of large insects in high-altitude layers around 400–800 m agl (3, 5, 33).

Next we summed the aerial-density values of the medium and large insects in each gate during each time-period, and then divided this value by the number of radar-sampling periods (~56 during the daytime, 8 during dusk, and ~32 during the night-time periods), and then by 15 (the number of altitude-bands). This value (X) is equal to the total aerial density of larger insects per 10^7 m³ on each day within the air column above each radar site. We converted these aerial-density values to a daily migration flow through a 1-km by 1-km (10^6 m²) ‘window’ above the radar, running west to east [and thus parallel to the principal migration directions during the spring and fall (Fig. 2A in main paper)]. This was achieved by the following procedure. Firstly, the migration flow through the 1-km² window each second (Y) was

calculated by: $Y \text{ (km}^{-2} \text{ s}^{-1}) = (X/10) \times \text{mean displacement speed (m s}^{-1})$. Secondly, the total migration flow through the 1-km² window in the daytime, dusk and night-time periods (Z) was calculated by: $Z \text{ (km}^{-2} \text{ day}^{-1}) = Y \times N \text{ seconds}$, where N is the number of seconds in the respective time period. The total migration flow values $\text{km}^{-2} \text{ day}^{-1}$ (Z) were used to calculate the mean daily migration flow of larger insects during the whole of the spring, summer and fall migration seasons, for each year and across all radar sites. To calculate the total seasonal movement over the study area (see Fig. 1A in the main paper), we extrapolated from the daily flow rates above each radar site to produce an estimate of the numbers crossing a line running west to east (i.e. perpendicular to the main migration direction which is north–south) along a 300-km stretch of the southern United Kingdom (table S2). Separate values were calculated for daytime, dusk and night-time periods, and then these were combined to produce a total value for the whole period (Fig. 1C and table S2). Using the individual body masses measured by the VLRs for every single larger insect, the migration intensities were then converted to biomass estimates for this size class (Fig S1 and table S3).

Calculation of high-altitude migration intensity and biomass of small insects (<10 mg)

Migration intensities of small insects cannot be monitored effectively with X-band VLRs; as explained above, those between 2–10 mg are sampled poorly (fig. S8b), while those <2 mg are not detected at all (14). Thus data on the high-altitude (>150 m agl) migration intensity of small insects must be obtained from sources other than entomological radar. We have extensive data on aerial densities of small insects from periods of aerial netting, carried out at 200 m agl at Cardington airfield in Bedfordshire (16), which was comparable with the altitude range of the VLRs. The aerial sampling indicated that cereal aphids and their parasitoid wasps (Hymenoptera: Braconidae) were the commonest day-flying small insects (16), while during dusk and night-time the small insects are mainly comprised of a variety of small Diptera, such as members of the Drosophilidae and various families of ‘midges’ (16). These small insects are typically more than two orders of magnitude more abundant than the larger (radar-detected) insects (fig. S8b), and so it is essential to estimate their abundance and combine these values with the radar-derived data on larger insects, in order to get a true picture of high-altitude aerial biomass and abundance.

Our aerial netting data, involving 256 separate samples taken during daytime, dusk and night-time periods, from 200 m above Cardington airfield during 1999 to 2007 (comprising 16,218 insects), in order to calculate the aerial density of all small insects (<10 mg body mass) at this altitude. We compared the mean aerial density values of the small insects caught by net at 200 m with the mean aerial densities of larger insects at the same altitude recorded by the VLRs on exactly the same days as aerial netting was carried out. From these data we determined that small insects (<10 mg) were 189 times more abundant than larger insects (10–500 mg) in the daytime, 154 times more abundant at dusk, and 348 times abundant at night. We therefore multiplied our VLR-generated measures of total migration intensity of larger insects over the 150–1200m height range by the factors above to produce the total migration intensity of small insects in each time-period, and then added the totals of small insects and larger insects to produce the overall total migration intensity in each time-period and across the entire 24-hour period (table S2).

Aerial density data from small insects caught in these aerial netting samples has been used, in combination with VLR-detected aerial densities of larger insects, to produce an aerial density–body

mass relationship across 4 orders of magnitude of body mass, from 0.1 mg to 1000 mg [see figure 7.4 in Drake and Reynolds (14) and figure 4 in Wood *et al.* (34), replicated here as fig. S8b]. We used the software program *GetData Graph Digitizer* (<http://www.getdata-graph-digitizer.com/>) to analyze the abundance-size relationship in fig. S8b, and calculated that the mean body mass of the small insects was 0.77 mg. We used this mass value to calculate the total biomass of all the small insects estimated to be airborne over the height range of 150–1200 m in each time-period (table S3).

Calculation of seasonal migratory directions

For each individual insect that passes through the beam, the VLR automatically records the migratory track (i.e. the displacement direction, which is largely determined by the wind but which is also influenced somewhat by the insect's flight vector), and the body alignment (the axis along which the insect's body is oriented) (14, 23). The body alignment has two possible values (the head-end and the tail-end of the insect), but the flight heading – the direction in which it would fly in the absence of wind – is presumed to be the value closest to the track direction (3, 31). The mean track (i.e. the migration direction) and the mean flight heading, plus associated circular statistics, were calculated for all 'mass migrations' of medium and large insects flying during the daytime and night-time periods (table S1) during all three seasons in the years 2000–2009.

For each mass migration, the following two parameters were calculated for the distributions of individual displacement directions and flight headings: (i) the mean direction; and (ii) the mean circular resultant length ' r ' (a measure of the clustering of the angular distribution of headings or displacements ranging from 0 to 1, with higher values indicating tighter clustering around the mean). Rayleigh's test of uniformity (35) was then used to test the null hypothesis that the distributions of headings and displacements followed a uniform distribution (an observed P -value of <0.05 indicates that the distribution is significantly unimodal, and hence the individual insects in that mass migration show a significant degree of common alignment of their displacements or headings). The great majority of migration events had unimodal distributions of displacement directions, reflecting the fact that they are strongly influenced by the wind which, during fair weather, is not expected to change its direction by any great degree over the course of the day. Those migration events exhibiting a statistically significant degree of common alignment of their headings were defined as showing "Common Orientation", and the proportion of the mass migrations showing this feature was calculated in each season / size category for daytime and night-time – values fell between 70–98% (table S1). Only those mass migrations with a unimodal distribution of tracks, and / or common orientation of their headings, were taken forward for further analysis to calculate the overall mean tracks and headings.

We then calculated the overall mean track and overall mean heading for each season / size category / time-period combination, by analyzing the individual mean values from all individual mass migrations (that were significantly unimodal) with the Rayleigh test once again (see Fig. 2A in the main paper, and table S5). If the overall distribution of mean tracks or mean headings was also significantly unimodal, we assumed that there was a preferred migration direction during this period; whereas if the distribution did not differ significantly from a uniform distribution, we assumed that there was no preferred migration direction during that period.

Downwind directions were also analyzed, but for every day and night (i.e. not just for the mass migration dates), to determine the seasonal patterns of prevailing winds. Downwind directions used in the seasonal analyses were the daily (or nightly) mean value from the altitude range of 150–1170 m agl (thus completely comparable with VLR sampling altitudes) during 10:00 – 18:00 UT (or 20:00 – 00:00 UT for night-time), obtained from the UK Met Office’s numerical weather prediction model, the “Unified Model” (36) (<http://www.metoffice.gov.uk/research/modelling-systems/unified-model>). Differences between the mean track and the mean downwind direction, and the mean heading and the mean downwind direction, for each group were analyzed with the Watson-Wheeler test (35) and the results are presented in table S5.

The migration directions of the small insects could not be directly measured because they are too small to be detected by our vertical-looking radars (14), and so we analyzed the distributions of downwind directions associated with mass migrations of dayflying aphids (the most abundant group of small insects). Aerial netting data provides a measure of high-altitude migration intensity of small insects (16), but data were too limited to carry out long-term seasonal comparisons. However, the log. aerial density of aphids (the main component of the small insect fauna) caught by aerial netting above Cardington was highly correlated with the log. density of aphids caught in a 12-m high Rothamsted Insect Survey suction trap (37) at Rothamsted (Pearson's product moment correlation coefficient (r) = 0.820, n = 48, P < 0.001; fig. S3A), and aphid data from the suction trap was available for every day. We then selected the aphid mass migrations in the same way as for the larger insects (i.e. by selecting the cumulative migration occasions which accounted for 75% of the total number of individual aphids in each season caught in the Rothamsted 12-m suction trap). Seasonal distributions of downwind directions (using outputs from the “Unified Model” (36) as above, but this time averaged over the lowest 100 m of the atmosphere during 10:00 – 18:00 UT) were then analyzed to see if there was any evidence of seasonally-beneficial tailwind selectivity in aphids (and, by proxy, in all small insects). Downwind directions during aphid mass migrations tended to be towards the north-east in all seasons, consistent with ‘dispersive’ movements on the prevailing south-westerly winds, albeit these patterns were only significant in the fall (Rayleigh tests; spring: mean direction = 66.6°, n = 112 mass migrations, circular resultant length (r) = 0.141, P = 0.107; summer: 71.9°, n = 78, r = 0.095, P = 0.493; fall: 56.0°, n = 147, r = 0.194, P = 0.004; fig. S4). Thus there was no evidence that aphids preferentially migrated on seasonally-beneficial winds as observed in the larger insects. As an additional check that small insect and larger insect migrations were not governed by exactly the same environmental drivers, we correlated the suction trap aphid aerial densities against radar-estimated larger insect aerial densities during the daytime. The results indicated that while the relationships between radar estimated migration flux and aphid density were positively correlated (medium insects: r = 0.349, n = 1430, P < 0.001; large insects: r = 0.298, n = 1242, P < 0.001), the low correlations and high degree of scatter (fig. S3B) indicate little association between the migration directions of the small insects and the larger insects. We therefore conclude that the small insects do not show seasonal preferences for migrating on seasonally-beneficial tailwinds, as would be expected for such weak-flying animals (38).

Calculation of net flows of biomass, nutrients and energy

For the calculation of net flows of biomass to the north in the spring, and the south in the fall (Fig. 3 in the main paper), we restricted our analyses to the radar-detected larger insects, as these were the only groups for which we had convincing evidence of seasonally-preferred migration directions. In each

season (spring and fall), the total biomass moving towards the north (defined as migratory tracks between 270° clockwise through 0° to 90°) were assigned a positive value, while the total biomass moving towards the south (defined as migratory tracks between 90° clockwise through 180° to 270°) were assigned a negative value. The sum of these values across the 24-hour daily period for both seasons produced the annual net flow of biomass towards the north or south (Fig. 3 in the main paper).

We calculated the total amounts of nitrogen (N) and phosphorus (P) in the annual insect movements in the following way. Based on the results of Finke (39) for house crickets *Acheta domesticus*, we assumed the migrating insects were composed of 69.2% water and 30.8% dry matter; thus, the 3200 tons of migrating insects represented 985.6 tons of dry matter. Insects are typically composed of 10% N by dry weight, and 1% P by dry weight, and thus the aerial movements involve 98,560 kg N and 9,856 kg P. These values represent the total quantity of these nutrients above the study area of 70,000 km², which equates to values of 0.00141 g m⁻² for N, and 0.000141 g m⁻² for P, deposited on the surface of the land from high-flying insect migrants falling out of the atmosphere. Atmospheric deposition of N over the whole of the UK has been estimated at 0.6655 g m⁻² (40), and so the input of N from the high-altitude insect migrants is 0.21% of that from other sources. Atmospheric deposition rates of P have been estimated to be between 0.003 and 0.022 g m⁻² (41, 42), and so the input of P from the high-altitude insect migrants is from 0.6% to 4.7% of that from other sources.

Based on data from Finke (39) for *A. domesticus*, we presumed that each kg of the dry mass of the high-altitude insect migrants contained 1402 kilocalories, which is equivalent to 5.87 million Joules per kg. For the 985.6 tons of dry mass estimated in this study to migrate above the region each year, this equates to 5.781 TerraJoules (5.781×10^{12} Joules).

Modelling effects of daytime surface-level meteorological variables on larger insect migration intensity

Linear mixed models (LMMs) fitted using residual maximum likelihood (REML) were used to investigate seasonal relationships (spring: $n = 748$; summer: $n = 470$; and autumn: $n = 881$) between the total daily count of all dayflying larger insects detected by the radar (common logarithm scale) and the following daytime surface-level weather variables: pressure, wind speed, temperature, relative humidity and wind direction. The latter was incorporated in cosine (cos) form, i.e. converted to a linear measure representing the degree of “northerliness / southerliness” of the wind, where 1 = blowing from the north, -1 = blowing from the south, and 0 = blowing from the east or west. Year and radar location (20 combinations in total: Malvern 2000 to 2003; Chilbolton 2004 to 2009; and Harpenden 2000 to 2009) were included as random effects (table S6).

To explore how daytime meteorological conditions affect the fine details of day-flying insect migration density, we used 15-min insect density estimates from the VLRs, and simulated wind speed, temperature and surface heat flux by the Regional Atmospheric Modeling System (RAMS) (43) at the exact spatial locations of the radars, run with a matching temporal resolution of 15 min. This numeric atmospheric modelling tool has been widely employed for atmospheric studies at various temporal and spatial scales, including bird and bat flight (44, 45). The finest grid of the model had a grid cell of 1 km \times 1 km, with grid center positioned at the exact radar location, for each of the three radars. For model input, we used the European Centre for Medium-Range Weather Forecasts (ECMWF) reanalysis, produced every six hours at a 0.125° spatial resolution worldwide. We coupled the 15 min model output

for wind speed, temperature and surface heat flux with the observed density recorded by the radar during specific time windows of 15 min, to temporally match the data. Using the total number of insects recorded for each body mass class in each 15 min period, we calculated separately for each body mass class from 10 mg to >200 mg the standardized proportions (so that they will sum up to 100%) of densities of larger insect migrants throughout the entire range of recorded atmospheric conditions prevailing during the period of the study (see fig. S5).

Calculation of total migration intensity and biomass of other taxa

For comparison with our measures of biomass, we also calculated the biomass involved in other, well-studied, migratory systems. The bogong moth *Agrotis infusa* is an Australian noctuid moth that makes an annual migration of up to 1000 km, from breeding grounds in southern Queensland, western and north-western New South Wales and western Victoria, to summer estivation sites in caves in the alpine regions of New South Wales and Victoria (7). Green (9, 46) has made a detailed study of this system, and estimates that 2.2 billion moths make the journey towards the caves each austral spring (46). Each adult moth weighs on average 326 mg (9), and so the total biomass of this migration is 717 t. Interestingly, an estimated 900 million estivating moths (294 t of biomass) are eaten by vertebrate predators from the cave sites each summer (9).

To estimate the total number of passerines (songbirds) migrating from Great Britain towards Africa each fall, we used the mid-range value of the total number of breeding adults of each species of migratory passerine in the whole of Great Britain reported in the third report of the Avian Population Estimates Panel (*APEP 3*) published in 2013 (47) and calculated the total number of migrating adults as comprising ~15 million individuals (table S8). Based on the findings of Hahn *et al.* (2), which indicated that adult breeders comprised 47% and recently fledged juveniles comprised 46% of all European migratory passerines during the fall migration, we assumed that the total number of fledged young taking part in the fall migration from Great Britain would be the same as the total number of breeding adults (table S8). We estimated the total biomass of this movement of 30 million birds by using the mean body mass values presented in the *Handbook of the Birds of the Western Palearctic* (48), and the total came to 415 t (table S8).

The number of monarch butterflies (*Danaus plexippus*) which annually migrate from their Eastern North American summer breeding grounds to their central Mexican wintering grounds has been estimated at 100–200 million individuals (1). We took the midpoint of this range (150 million individuals), and assumed that the average mass of each individual was 500 mg based on data in Fig. 3 of Altizer and Oberhauser (49). This produced a value of 75 t for the total biomass of the Eastern North American fall migratory population.

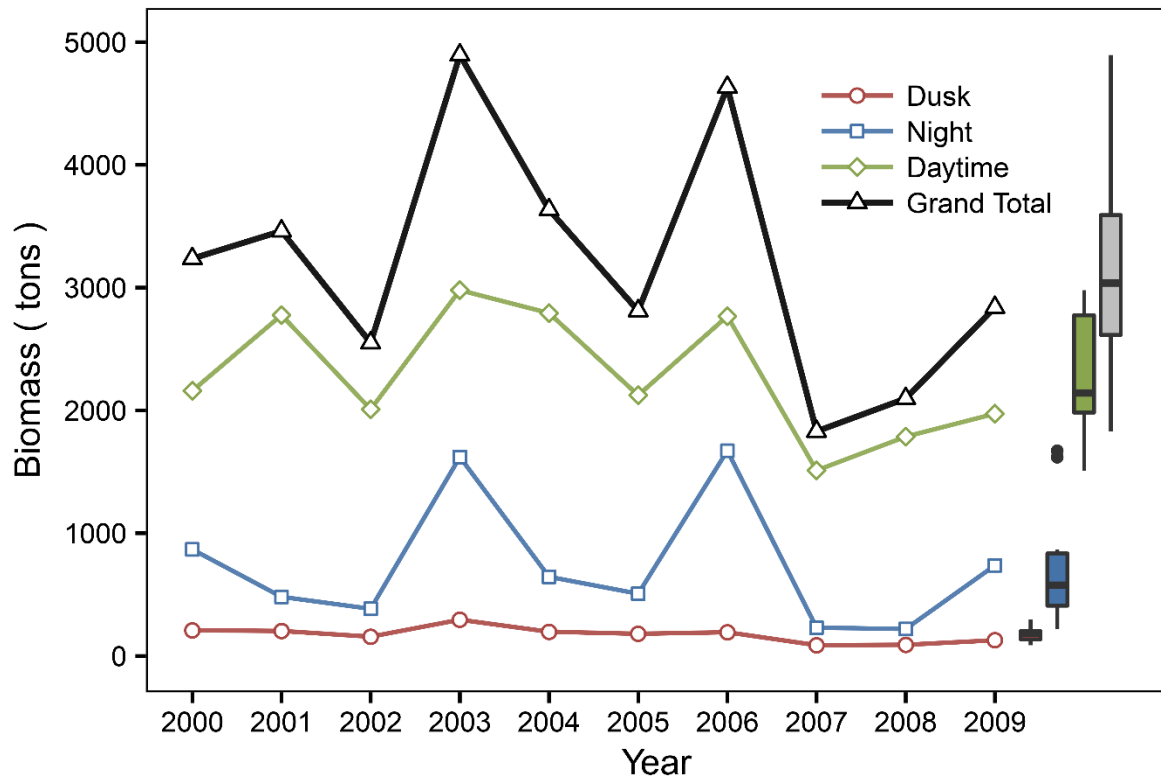


Fig. S1. Annual patterns of total biomass of all insects migrating above the study region. The data is shown for daytime, dusk and night-time periods separately (colored lines and boxes) and combined for the whole 24-hour period (black line and grey box). For the box plots on the right, central bars represent median values, boxes represent 25th to 75th percentiles (interquartile range, IQR), whiskers extend to observations within ± 1.5 times the IQR, and dots show the outliers.

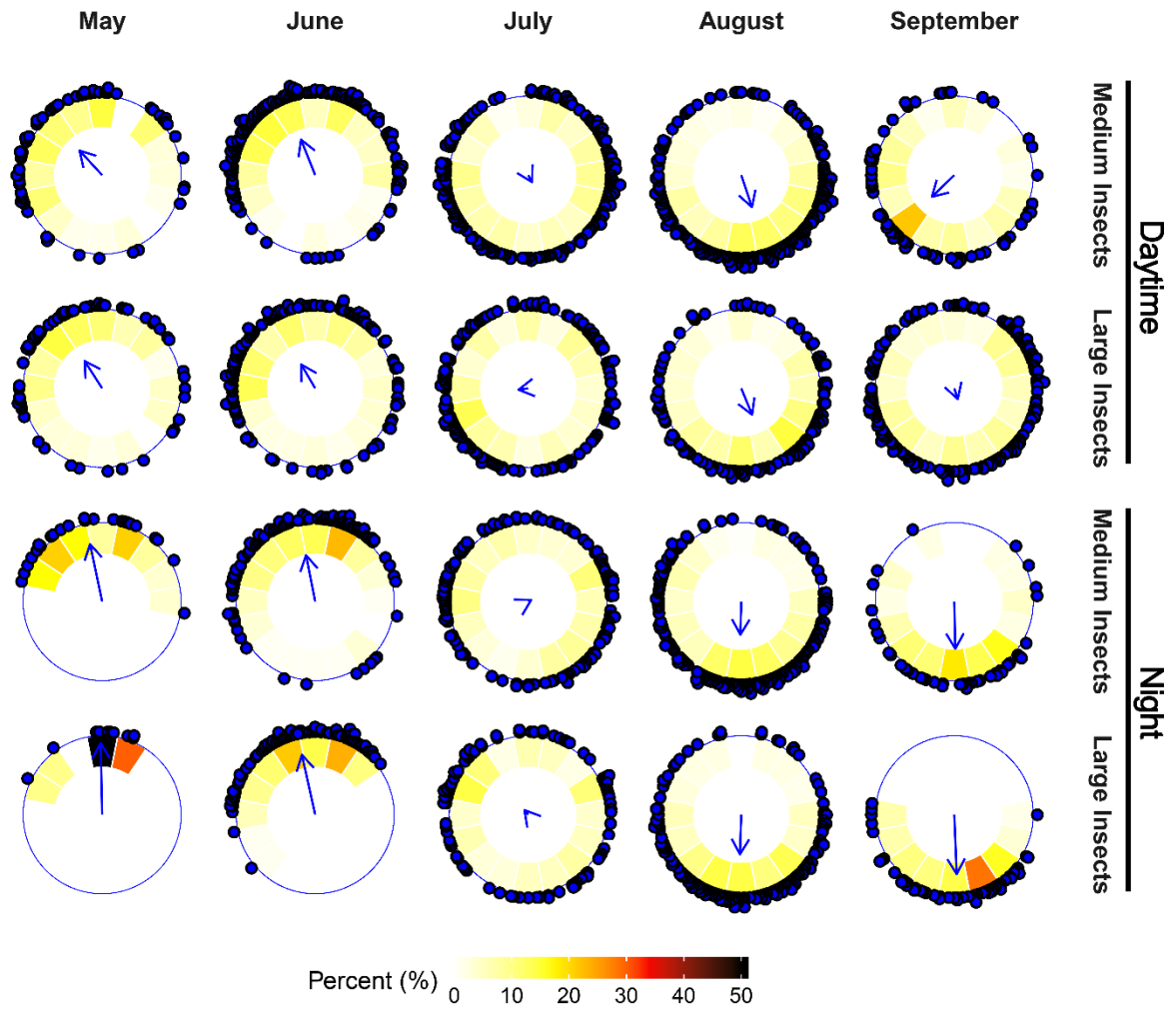


Fig. S2. Monthly track directions of larger insects migrating high above the southern United Kingdom. Migratory tracks of larger insects occurred predominantly in seasonally-beneficial directions in May and June, and in August and September, but were randomly directed in July. Small blue circles on the periphery of the circular histograms represent the mean track direction of mass migrations, and the color bar indicates the percentage of the total in each 22.5° bin. The bearing of the blue arrow indicates the overall mean direction of the dataset, and arrow length is proportional to the degree of clustering of the individual directions around the mean (the circular resultant length, or r -value). Based on these results, we designated May and June as ‘spring’, July as ‘summer’, and August and September as ‘fall’. Statistics are presented in table S4.

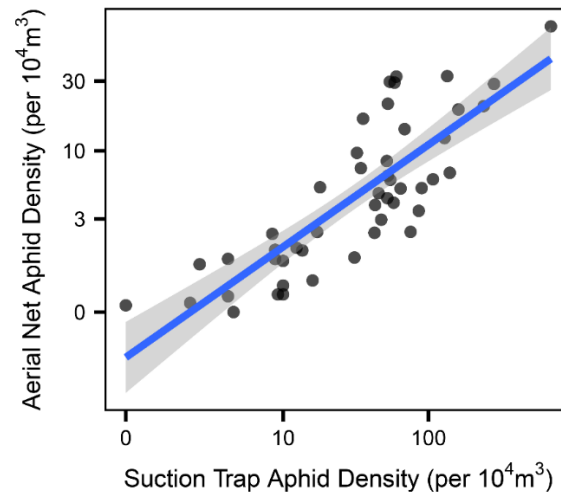
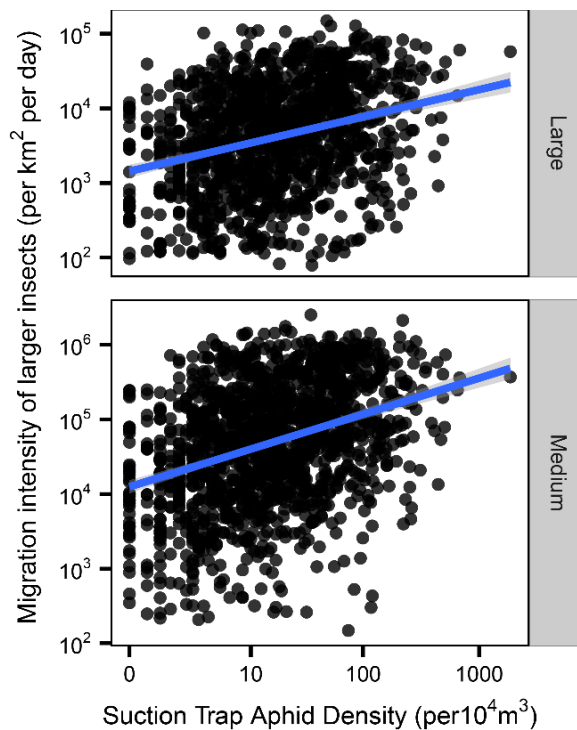
A**B**

Fig. S3. Association of intensity of aphid migrations with migrations of larger insects. (A) Daily aerial densities (on \log_{10} scale) of aphids sampled with a balloon-supported net 200 m above the ground in central Bedfordshire (16) are highly correlated with the aerial density (on \log_{10} scale) of aphids sampled with a 12 m suction trap (37) at Rothamsted (35 km to the south) on the same day (Pearson's product moment correlation coefficient (r) = 0.820), albeit at about one-tenth of the absolute value. We assumed that aphids, as the most abundant constituent of the small aerial insect fauna (16), are representative of the entire small insect fauna. We also examined the degree of association between migration intensity of radar-detected larger insects and migration intensity of aphids caught by the Rothamsted suction trap (B). Correlations (\log_{10} - \log_{10} scale) were positive in both cases (medium-sized insects versus aphids: r = 0.349; large insects versus aphids: r = 0.089), but with a high degree of scatter, indicating that aphid migrations and those of the larger insects were not affected by the same combination of environmental drivers.

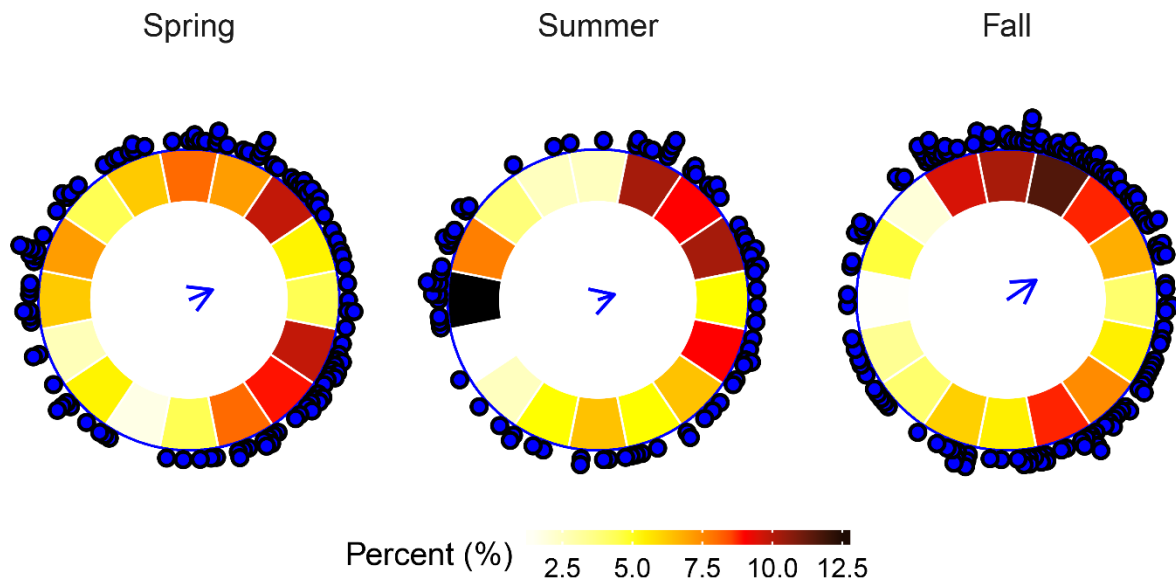


Fig. S4. Downwind directions associated with mass seasonal migrations of aphids. Based on the data presented in fig. S3A, we used aphid abundance in the 12-m high suction trap at Rothamsted as a proxy for the high-altitude migration intensity of all small insects. The mean downwind direction in the lowest 100 m of the atmosphere during each aphid mass migration was analyzed separately for each season. Downwind directions during aphid mass migrations most commonly blew towards the north-east (Rayleigh tests; spring: mean direction = 66.6° , $n = 112$ mass migrations, circular resultant length (r) = 0.141, $P = 0.107$; summer: 71.9° , $n = 78$, $r = 0.095$, $P = 0.493$; fall: 56.0° , $n = 147$, $r = 0.194$, $P = 0.004$), similar to the prevailing downwind directions. The migration directions of the small insects would also have tended to be towards the north-east in all seasons, as aphids (and other small insects) are not capable of deflecting their migratory track direction from the flow direction (38). Small blue circles on the periphery of the circular histograms represent the downwind directions associated with each aphid mass migration in each season, and the color bar indicates the percentage of the total in each 22.5° bin. The bearing of the blue arrow indicates the overall mean direction of the dataset, and arrow length is proportional to the degree of clustering of the individual directions around the mean (the circular resultant length, or r -value).

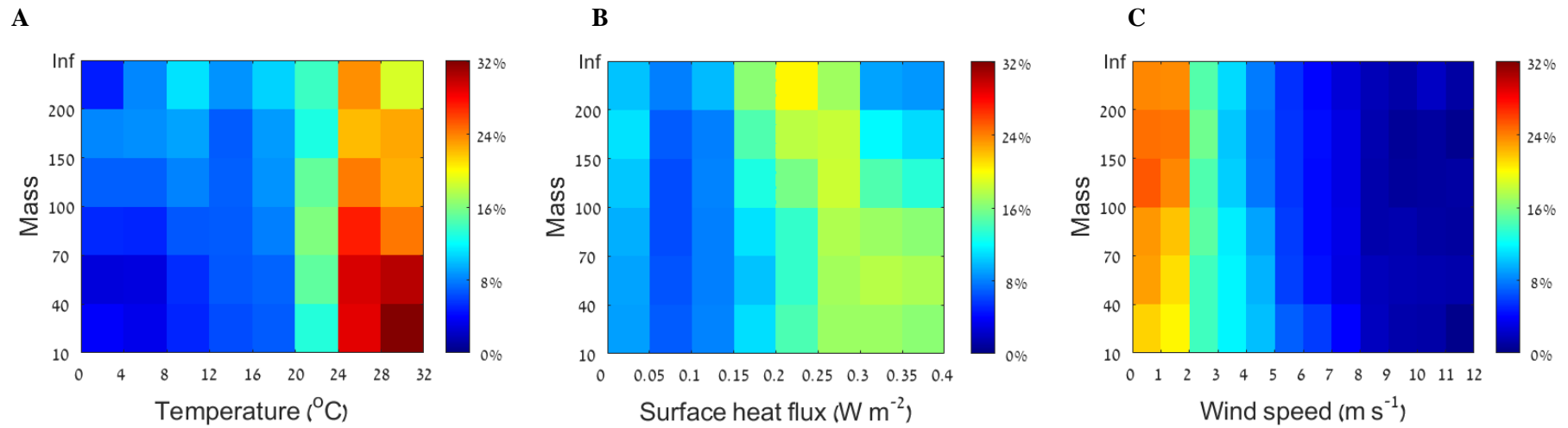


Fig. S5. Relationship between ground-level meteorological variables and migration intensity above southern United Kingdom. Higher proportions of larger insect mass migrations (color scale bars) were associated with warmer temperatures (A), intermediate and high levels of surface heat flux (B), and slower wind speeds (C).

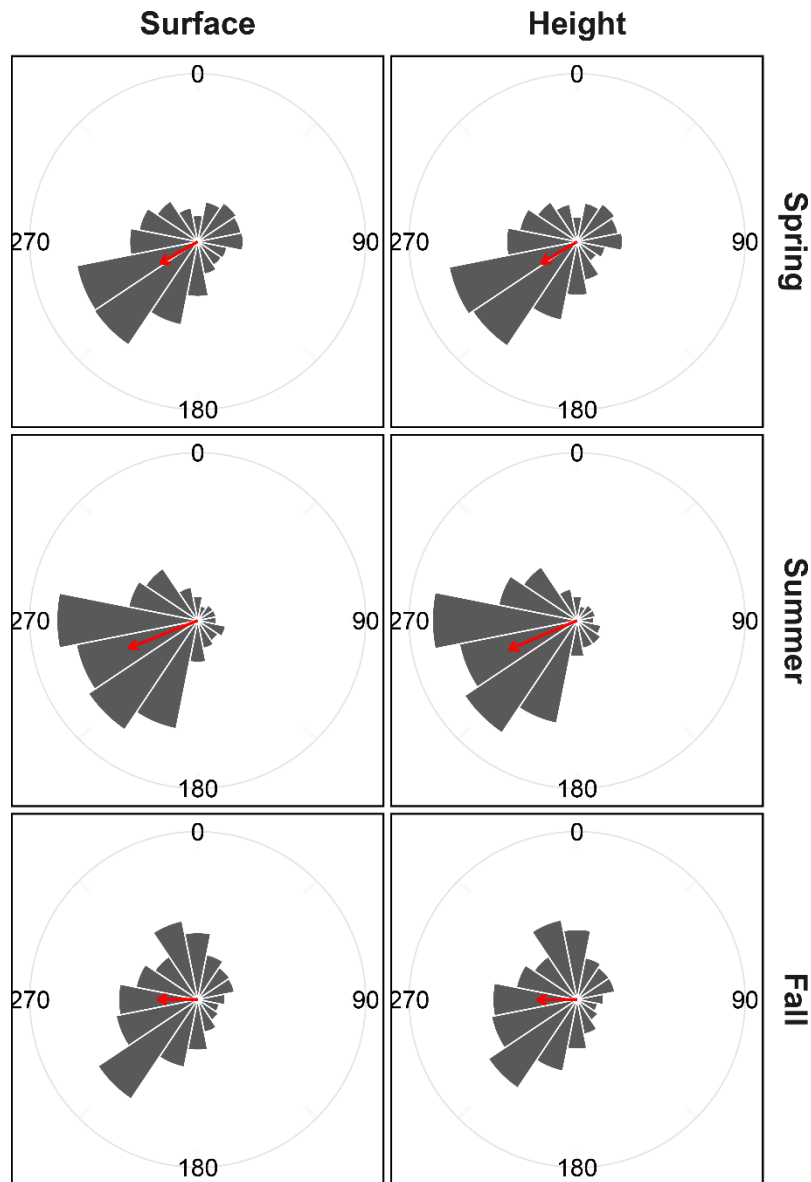


Fig. S6. Circular histograms of daytime wind directions at the surface and at height (150–350 m above the ground). Note wind directions are shown here in the conventional meteorological way (i.e. the direction the wind is blowing from, *not* the downwind direction). The area of the black segments is proportional to the number of occasions when wind directions fell within each 22.5° bin. The bearing of the red arrow indicates the mean direction, while its length is proportional to the clustering of the directions around the mean. Surface and high-altitude wind directions were strongly correlated in spring ($\rho_T = 0.992$, $n = 748$, $P < 0.001$; **top row**), summer ($\rho_T = 0.997$, $n = 470$, $P < 0.001$; **middle row**), and fall ($\rho_T = 0.993$, $n = 881$, $P < 0.001$; **bottom row**), and consistently blew from the southwest to the northeast.

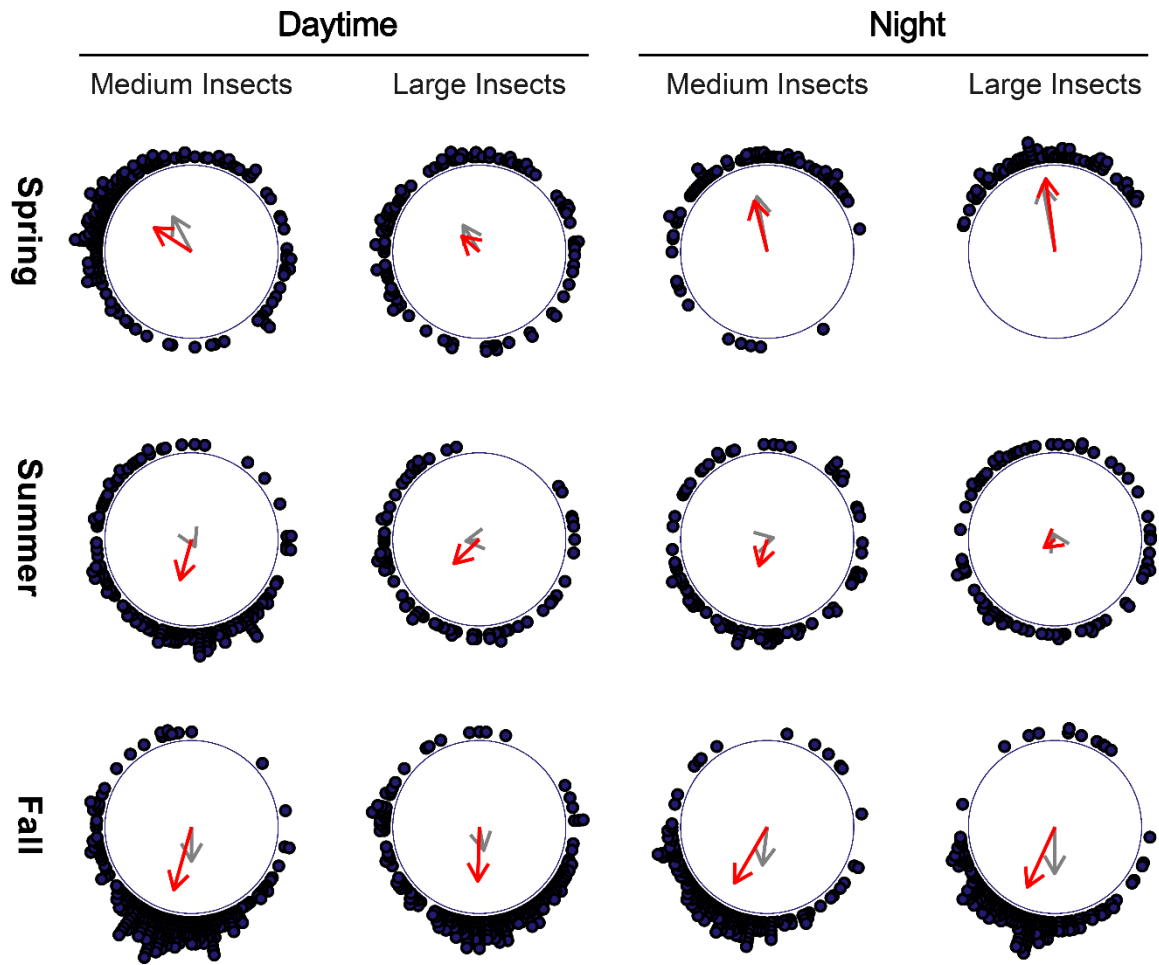


Fig. S7. Comparison of seasonal heading and track directions of larger insects high above the southern United Kingdom. Migratory headings (red arrows) of larger insects occurred predominantly in seasonally-beneficial directions in the spring and fall, when they were also very similar to the track directions (grey arrows). Small black circles on the periphery of the circular histograms represent the mean heading of mass migrations. The bearing of the red arrow indicates the overall mean heading of the dataset, and arrow length is proportional to the degree of clustering of the individual headings around the mean (the circular resultant length, or r -value). For comparative purposes, mean track directions (grey arrows) are presented too (see Fig. 2A in main paper). Heading statistics are presented in table S7.

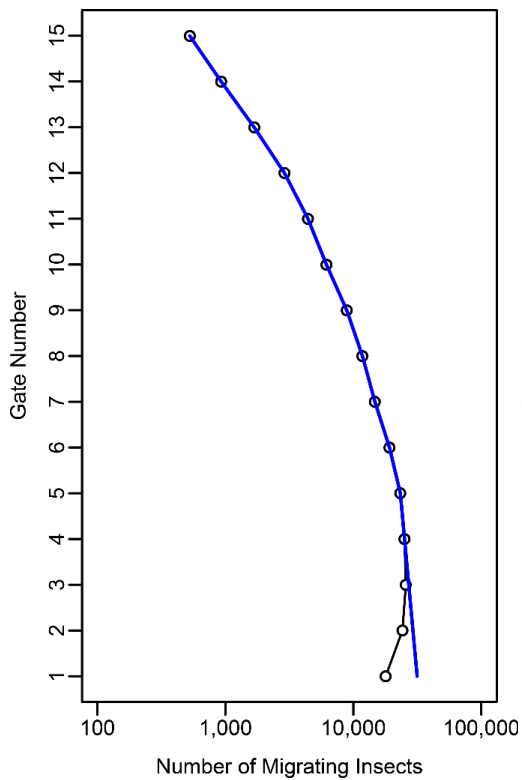
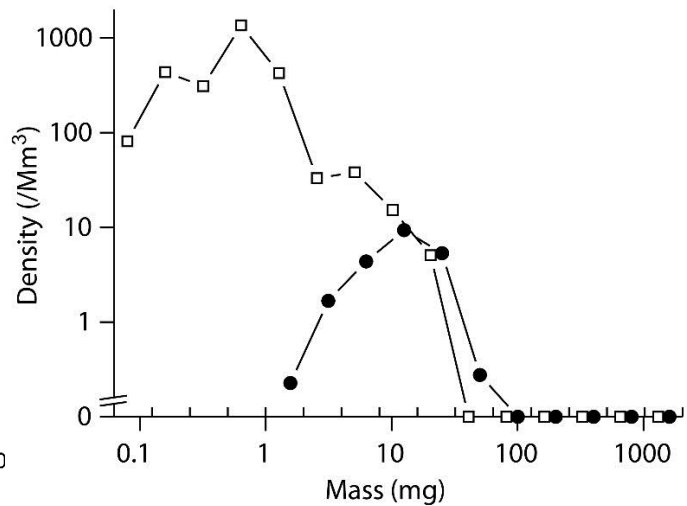
A**B**

Fig. S8. Aerial density relationships. (A) Density-height relationship for medium dayflying insects (black line and open circles), and the log-linear regression (blue line) based on data in altitude bands 15 down to 4, and then extrapolated to estimate the actual values in altitude bands 1 to 3. These values were used to correct the observed values in this size category and time period (see Fig. S1B in main paper). (B). Average daytime aerial densities (per million m³ plotted on a log₁₀ scale) of insects sampled with a balloon-supported net 200 m above the ground in central Bedfordshire (open squares) and from the lowest altitude band of the Rothamsted VLR operated nearby (closed circles), for a series of insect mass categories (plotted on a log₁₀ scale). Aerial catches and radar data are mean values from several July (i.e. midsummer) days. The plot shows that small insects (<10 mg) are >2 orders of magnitude more abundant than larger insects (10–500 mg), and also that VLRs do not adequately detect insects <10 mg in body mass. The mean mass of the small insect category is around 0.8 mg. Reproduced with permission from Drake and Reynolds (14).

Table S1. Total number of migration occasions, number of ‘mass migrations’, and numbers of individual larger insects detected by the VLRs. The proportion of the mass migrations which exhibited a significant degree of common orientation (see *Methods*) is also presented. Mass migrations are defined as the subset of occasions which cumulatively account for 75% of the total number of individuals in each season/size category combination.

Time Period	Insect Category	Season	Number of Migration Occasions		Number of Insects		Common Orientation
			All	‘Mass Migrations’	All	‘Mass Migrations’	
Daytime	Large (70–500 mg)	Spring	869	185 (21%)	35,080	26,281 (75%)	70%
		Summer	553	145 (26%)	31,802	23,825 (75%)	70%
		Fall	1,060	292 (28%)	48,555	36,388 (75%)	82%
		<i>Subtotal</i>	2,482	622 (25%)	115,437	86,494 (75%)	74%
	Medium (10–70 mg)	Spring	1,067	221 (21%)	397,170	297,358 (75%)	96%
		Summer	604	186 (31%)	607,247	454,312 (75%)	99%
		Fall	1,155	291 (25%)	547,320	410,332 (75%)	98%
		<i>Subtotal</i>	2,826	698 (25%)	1,551,737	1,162,002 (75%)	98%
	Grand Total	All	5,308	1,320 (25%)	1,667,174	1,248,496 (75%)	
	Night-time	Large (70–500 mg)	Spring	823	94 (11%)	30,889	23,124 (75%)
Summer			571	90 (16%)	33,279	24,930 (75%)	91%
Fall			1,088	222 (20%)	43,280	32,426 (75%)	95%
<i>Subtotal</i>			2,482	406 (16%)	107,448	80,480 (75%)	95%
Medium (10–70 mg)		Spring	766	133 (17%)	12,841	9,628 (75%)	73%
		Summer	558	125 (22%)	18,996	14,212 (75%)	77%
		Fall	1,070	234 (22%)	28,815	21,603 (75%)	87%
		<i>Subtotal</i>	2,394	492 (21%)	60,652	45,443 (75%)	79%
Grand Total		All	4,876	898 (18%)	168,100	125,923 (75%)	86%

Table S2. Seasonal and annual abundance of all migratory insects over the southern United Kingdom.

Year	Total number ($\times 10^9$) of all insects				Total number ($\times 10^9$) of medium (10–70 mg) insects				Total number ($\times 10^9$) of large (70–500 mg) insects			
	Daytime	Dusk	Night	Total	Daytime	Dusk	Night	Total	Daytime	Dusk	Night	Total
2000	2297	210	828	3335	11.42	1.22	1.14	13.78	0.67	0.14	1.23	2.04
2001	3030	215	495	3741	15.48	1.33	0.94	17.75	0.46	0.06	0.48	1.00
2002	2116	167	379	2663	10.33	1.03	0.64	12.01	0.81	0.05	0.44	1.30
2003	3201	290	1514	5005	16.22	1.65	2.03	19.89	0.63	0.22	2.31	3.16
2004	2898	203	665	3766	14.38	1.24	1.39	17.00	0.88	0.07	0.52	1.46
2005	2259	193	511	2963	11.31	1.20	0.99	13.49	0.59	0.04	0.48	1.11
2006	3009	187	1591	4787	15.27	1.00	1.78	18.06	0.57	0.20	2.78	3.55
2007	1598	94	227	1918	7.86	0.58	0.40	8.84	0.54	0.03	0.25	0.82
2008	1983	99	231	2313	10.15	0.62	0.47	11.23	0.29	0.02	0.20	0.50
2009	2267	137	807	3211	11.78	0.84	1.84	14.46	0.15	0.05	0.47	0.67
Mean	2466	180	725	3370	12.42	1.07	1.16	14.65	0.56	0.09	0.92	1.56
<i>±1 S.E.M.</i>	<i>169</i>	<i>19</i>	<i>153</i>	<i>314</i>	<i>0.87</i>	<i>0.10</i>	<i>0.18</i>	<i>1.10</i>	<i>0.07</i>	<i>0.02</i>	<i>0.29</i>	<i>0.33</i>
% of All Insects	73.17%	5.33%	21.51%	100%	0.50%	0.60%	0.16%	0.43%	0.02%	0.05%	0.13%	0.05%

Table S3. Seasonal and annual biomass of all migratory insects over the southern United Kingdom.

Year	Total biomass (tons) of all insects				Total biomass (tons) of medium (10–70 mg) insects				Total biomass (tons) of large (70–500 mg) insects			
	Daytime	Dusk	Night	Total	Daytime	Dusk	Night	Total	Daytime	Dusk	Night	Total
2000	2159	209	868	3236	309.25	26.56	33.27	369.09	85.63	20.87	197.51	304.00
2001	2776	204	481	3461	390.46	29.38	23.15	442.99	58.13	9.00	76.87	144.00
2002	2008	157	384	2549	287.13	21.91	17.11	326.15	95.66	6.80	75.27	177.73
2003	2979	295	1620	4894	442.63	38.49	53.29	534.41	77.62	34.43	401.23	513.28
2004	2792	197	645	3634	448.92	30.53	31.89	511.33	117.37	10.57	101.00	228.95
2005	2123	181	507	2810	312.62	25.83	22.18	360.63	74.95	7.08	91.20	173.23
2006	2767	193	1672	4632	386.70	23.23	59.58	469.52	69.08	26.43	387.43	482.94
2007	1511	88	230	1829	208.87	11.87	9.70	230.44	74.79	3.86	46.02	124.68
2008	1786	91	220	2096	227.92	12.31	12.68	252.92	34.70	2.80	29.37	66.88
2009	1972	128	738	2838	217.49	18.89	74.16	310.54	13.68	4.11	42.40	60.19
Mean	2287	174	737	3198	323.20	23.90	33.70	380.80	70.16	12.60	144.83	227.59
<i>±1 S.E.M.</i>	<i>159</i>	<i>20</i>	<i>165</i>	<i>316</i>	<i>28.59</i>	<i>2.60</i>	<i>6.86</i>	<i>33.30</i>	<i>9.32</i>	<i>3.43</i>	<i>44.12</i>	<i>50.50</i>
% of All Insects	71.52%	5.45%	23.03%	100%	14.13%	13.72%	4.58%	11.91%	3.07%	7.23%	19.66%	7.12%

Table S4. Monthly track directions of larger insects migrating high above southern United Kingdom (see fig. S2). On occasions when distributions of track directions were not significantly unimodal (in July), an overall mean direction has not been calculated. Non-significant *P*-values are highlighted in bold text, and mean directions are not presented if the Rayleigh test was non-significant.

Time Period	Month	Size	<i>n</i>	Mean direction	<i>r</i>	<i>P</i>
Daytime	May	Medium insects	61	317.34	0.422	<0.0001
Daytime	May	Large insects	61	327.37	0.409	<0.0001
Daytime	June	Medium insects	160	338.21	0.483	<0.0001
Daytime	June	Large insects	124	329.56	0.350	<0.0001
Daytime	July	Medium insects	186	-	0.101	0.153
Daytime	July	Large insects	145	-	0.123	0.112
Daytime	August	Medium insects	222	161.47	0.426	<0.0001
Daytime	August	Large insects	121	157.69	0.361	<0.0001
Daytime	September	Medium insects	69	225.94	0.394	<0.0001
Daytime	September	Large insects	171	162.27	0.143	0.0309
Night	May	Medium insects	24	348.09	0.742	<0.0001
Night	May	Large insects	10	358.82	0.905	<0.0001
Night	June	Medium insects	109	348.83	0.598	<0.0001
Night	June	Large insects	84	347.50	0.775	<0.0001
Night	July	Medium insects	125	-	0.043	0.793
Night	July	Large insects	90	-	0.077	0.589
Night	August	Medium insects	191	181.52	0.419	<0.0001
Night	August	Large insects	166	181.91	0.500	<0.0001
Night	September	Medium insects	43	178.81	0.597	<0.0001
Night	September	Large insects	56	177.68	0.752	<0.0001

Table S5. Seasonal patterns of downwind directions during all occasions, and the migratory tracks of the larger insects during “mass migrations” (see *Methods*), analyzed using the Rayleigh test for ‘spring’ (May and June), ‘summer’ (July) and ‘fall’ (August and September). Differences between migratory tracks and overall downwind directions were tested with the Watson-Wheeler test. Non-significant *P*-values are highlighted in bold text, and mean directions are not presented if the Rayleigh test was non-significant.

Time period	Season		<i>n</i>	Rayleigh test			Watson-Wheeler test		
				Mean Direction	<i>r</i>	<i>P</i>	<i>w</i>	<i>P</i>	
Daytime	Spring	Downwind direction	910	59.69	0.292	<0.0001			
	Spring	Track (Medium Insects)	221	333.04	0.461	<0.0001	107.3	<0.0001	
	Spring	Track (Large Insects)	185	328.76	0.369	<0.0001	77.3	<0.0001	
	Summer	Downwind direction	519	66.01	0.495	<0.0001			
	Summer	Track (Medium Insects)	186	-	0.101	0.153	55.3	<0.0001	
	Summer	Track (Large Insects)	145	-	0.123	0.112	64.9	<0.0001	
	Fall	Downwind direction	978	84.22	0.281	<0.0001			
	Fall	Track (Medium Insects)	291	174.47	0.375	<0.0001	85.57	<0.0001	
	Fall	Track (Large Insects)	292	159.33	0.233	<0.0001	35.50	<0.0001	
	Night-time	Spring	Downwind direction	900	68.99	0.245	<0.0001		
		Spring	Track (Medium Insects)	133	348.67	0.624	<0.0001	118.8	<0.0001
		Spring	Track (Large Insects)	94	348.87	0.787	<0.0001	134.0	<0.0001
Summer		Downwind direction	517	81.49	0.433	<0.0001			
Summer		Track (Medium Insects)	125	-	0.043	0.793	26.6	<0.0001	
Summer		Track (Large Insects)	90	-	0.077	0.589	31.5	<0.0001	
Fall		Downwind direction	969	101.31	0.260	<0.0001			
Fall		Track (Medium Insects)	234	180.87	0.452	<0.0001	80.0	<0.0001	
Fall		Track (Large Insects)	222	180.49	0.563	<0.0001	109.5	<0.0001	

Table S6. Results of linear mixed models (LMMs) fitted using residual maximum likelihood (REML), including 5 explanatory surface weather variables. The response variable was the \log_{10} transformation of the total daily count of all larger insects detected. Wind direction was incorporated as the cosine (cos) of the wind direction, to convert to a linear measure representing the degree of “northerliness / southerliness” of the wind, where 1 = blowing from the north, -1 = from the south, and 0 = from the east or west. Relationships were typically positive for temperature and pressure, negative for wind speed and humidity, indicating high levels of migration on warm, settled, dry days. During spring, migration was greatest on days when winds had a large component of “southerliness” (blowing from the south; thus the slope was negative, and was not far from statistical significance at the 5% level); during the fall, migration was greatest on days when winds had a large component of “northerliness” (blowing from the north; thus the slope was positive, and was statistically significant). The *F*-statistics, degrees of freedom (*DF*; rounded to the nearest integer) and *P*-values given here are those for dropping the given term from the full model with all 5 explanatory variables included. Slopes and their standard errors are from the full model.

Season	Fixed Term	<i>F</i>	<i>DF</i>	<i>P</i>	Slope	S.E. (Slope)
Spring	Pressure	18.83	1, 724	<0.001	0.0128	0.0030
Spring	Temperature	353.06	1, 742	<0.001	0.1076	0.0057
Spring	Relative Humidity	30.77	1, 740	<0.001	-0.0081	0.0015
Spring	Wind Speed	32.33	1, 738	<0.001	-0.0597	0.0105
Spring	Cos (Wind Direction)	3.19	1, 742	0.074	-0.0569	0.0318
Summer	Pressure	25.20	1, 450	<0.001	0.0227	0.0045
Summer	Temperature	172.38	1, 463	<0.001	0.1279	0.0097
Summer	Relative Humidity	2.02	1, 462	0.156	-0.0035	0.0025
Summer	Wind Speed	10.73	1, 457	0.001	-0.0539	0.0165
Summer	Cos (Wind Direction)	0.14	1, 458	0.713	-0.0157	0.0427
Fall	Pressure	0.05	1, 865	0.822	0.0007	0.0029
Fall	Temperature	322.94	1, 868	<0.001	0.1144	0.0064
Fall	Relative Humidity	41.07	1, 872	<0.001	-0.0103	0.0016
Fall	Wind Speed	63.44	1, 872	<0.001	-0.0869	0.0109
Fall	Cos (Wind Direction)	129.58	1, 866	<0.001	0.3078	0.0270

Table S7. Seasonal heading distributions and displacement speeds of large and medium-sized insects. Displacement speeds are means ± 1 standard error of the mean (SEM) of all individuals in each season / size combination measured by the VLRs; they represent the combined wind vector (wind speed and downwind direction) and self-powered flight vector (insect airspeed and heading). Data for headings are presented in fig. S7 and speeds are presented in Fig. 2B in the main paper.

Time Period	Size Category	Season	Number of Mass Migrations	Heading	Circular Resultant Length (<i>r</i>)	<i>P</i>	Mean Displacement Speed ± 1 SEM (m/s)	Mean Displacement Speed (km/h)
Daytime	Large Insects	Spring	105	311.46	0.269	0.0005	13.83 \pm 0.34	50
Daytime	Large Insects	Summer	72	226.22	0.404	<0.0001	12.46 \pm 0.27	45
Daytime	Large Insects	Fall	204	181.69	0.626	<0.0001	11.22 \pm 0.24	40
Daytime	Medium Insects	Spring	169	302.68	0.511	<0.0001	11.62 \pm 0.23	42
Daytime	Medium Insects	Summer	143	195.59	0.483	<0.0001	10.55 \pm 0.19	38
Daytime	Medium Insects	Fall	244	195.73	0.753	<0.0001	9.97 \pm 0.18	36
Night	Large Insects	Spring	73	352.79	0.849	<0.0001	16.47 \pm 0.48	59
Night	Large Insects	Summer	78	232.23	0.156	0.1510	13.02 \pm 0.37	47
Night	Large Insects	Fall	183	204.70	0.763	<0.0001	14.16 \pm 0.27	51
Night	Medium Insects	Spring	74	345.68	0.604	<0.0001	13.99 \pm 0.43	50
Night	Medium Insects	Summer	90	196.85	0.319	0.0001	12.67 \pm 0.35	46
Night	Medium Insects	Fall	161	210.26	0.749	<0.0001	12.72 \pm 0.27	46

Table S8. Population size (breeding adults plus fledged young in each year), and total biomass, of all migratory passerines which depart Great Britain on fall migration towards Africa. Population estimates of breeding pairs come from the most recent report of the Avian Population Estimates Panel (47); the average proportion of fledged young in the total population of migrants is presumed to be 50% based on the work of Hahn *et al.* (2); and body mass estimates were taken from the *Birds of the Western Palearctic* (48).

Species	Scientific Name	Adults	Fledged	Total	Body Mass (g)	Total Biomass (kg)
Sand Martin	<i>Riparia riparia</i>	210,000	210,000	420,000	13.5	5670
Swallow	<i>Hirundo rustica</i>	1,520,000	1,520,000	3,040,000	19	57760
House Martin	<i>Delichon urbica</i>	510,000	510,000	1,020,000	19	19380
Wood Warbler	<i>Phylloscopus sibilatrix</i>	13,000	13,000	26,000	10	260
Chiffchaff	<i>Phylloscopus collybita</i>	2,000,000	2,000,000	4,000,000	8	32000
Willow Warbler	<i>Phylloscopus trochilus</i>	4,400,000	4,400,000	8,800,000	9.5	83600
Blackcap	<i>Sylvia atricapilla</i>	2,200,000	2,200,000	4,400,000	20.5	90200
Garden Warbler	<i>Sylvia borin</i>	340,000	340,000	680,000	19	12920
Lesser Whitethroat	<i>Sylvia curruca</i>	148,000	148,000	296,000	12	3552
Common Whitethroat	<i>Sylvia communis</i>	2,200,000	2,200,000	4,400,000	15.5	68200
Grasshopper Warbler	<i>Locustella naevia</i>	26,000	26,000	52,000	13.5	702
Sedge Warbler	<i>Acrocephalus schoenobaenus</i>	520,000	520,000	1,040,000	12	12480
Reed Warbler	<i>Acrocephalus scipaceus</i>	130,000	130,000	260,000	13	3380
Ring Ouzel	<i>Turdus torquatus</i>	6,850	6,850	13,700	115	1575.5
Spotted Flycatcher	<i>Muscicapa striata</i>	66,000	66,000	132,000	17	2244
Common Nightingale	<i>Luscinia megarhynchos</i>	13,400	13,400	26,800	20.5	549.4
Pied Flycatcher	<i>Ficedula hypoleuca</i>	18,500	18,500	37,000	12.5	462.5
Common Redstart	<i>Phoenicurus phoenicurus</i>	100,000	100,000	200,000	14.5	2900
Whinchat	<i>Saxicola rubetra</i>	47,000	47,000	94,000	16.5	1551
Common Wheatear	<i>Oenanthe oenanthe</i>	230,000	230,000	460,000	23.5	10810
Yellow Wagtail	<i>Motacilla flava</i>	30,000	30,000	60,000	17.5	1050
Tree Pipit	<i>Anthus trivialis</i>	88,000	88,000	176,000	23.5	4136
TOTAL				29,633,500		415,382

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