Seasonal migration to high latitudes results in major reproductive benefits in an insect

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Little is known of the population dynamics of long-range insect migrants, and it has been suggested that the annual journeys of billions of nonhardy insects to exploit temperate zones during summer represent a sink from which future generations seldom return (the "Pied Piper" effect). We combine data from entomological radars and ground-based light traps to show that annual migrations are highly adaptive in the noctuid moth *Autographa gamma* (silver Y), a major agricultural pest. We estimate that 10–240 million immigrants reach the United Kingdom each spring, but that summer breeding results in a fourfold increase in the abundance of the subsequent generation of adults, all of which emigrate southward in the fall. Trajectory simulations show that 80% of emigrants will reach regions suitable for winter breeding in the Mediterranean Basin, for which our population dynamics model predicts a winter carrying capacity only 20% of that of northern Europe during the summer. We conclude not only that poleward insect migrations in spring result in major population increases, but also that the persistence of such species is dependent on summer breeding in high-latitude regions, which requires a fundamental change in our understanding of insect migration.

windborne migration | source-sink dynamics

Migration arises when the reproductive benefits accrued from moving exceed those of remaining in the current habitat (1). Numerous insect species, comprising members of several insect orders, migrate poleward from lower-latitude winter habitats each spring to exploit temporary resources where they can reproduce during the summer but are unable to survive over winter (2–9). Compared with our knowledge of the energetic costs, mortality risks, and reproductive benefits of bird migration (10–16), the adaptive benefits and population dynamics consequences of insect migration are poorly understood (6–9). For most migratory insects, their low-latitude winter habitats are considered to be the major breeding grounds. In fact, some authors have previously suggested that seasonal poleward shifts to exploit temperate ecosystems represent a population sink from which progeny seldom returned: a phenomenon known as the "Pied Piper" effect (17, 18). This notion made little evolutionary sense, however, and has been contested (7, 8, 19); moreover, return flights have been observed in many species (5, 7–9, 20–25). However, it is unclear whether high-latitude breeding results in net reproductive benefits to migrating species or whether significant proportions of the progeny produced over the summer successfully make it back to regions where they can breed again, and there is no information on population sizes and migration intensities between zones. These are vital issues because billions of insects immigrate annually to, or within, the temperate zone, providing major ecosystem services as well as, in some cases, causing serious crop damage and spreading diseases of humans and their livestock (9).

Here we combine analyses of long-term field data, migration trajectory simulations, and population dynamic modeling to study these questions in the Palaearctic noctuid moth *Autographa gamma* (the silver Y). This abundant moth is a major pest of a range of crops, including beet, potato, maize, brassica, and legumes, that breeds continuously with five or more generations per year (26). Spring migrants use fast-moving airstreams, 200–1,000 m above ground, to travel ~300 km northward per night to colonize temporary summer-breeding grounds in northern Europe (22–25), from their winter-breeding grounds in North Africa and the Middle East (27–30). This species cannot survive the winter in the United Kingdom or similar latitudes in northern Europe (31), and all of the evidence indicates that only small remnant populations can survive through the hot and dry summers of its wintering areas (27–30) (*Results*). There is evidence that at least some of the progeny of summer breeders embark on southward-directed migrations in the fall (22–25), but there is no evidence as yet that these migrants regularly reach the winter-breeding areas or what proportion of the summer population engages in return migration. Thus, there are two competing hypotheses that could explain the annual recolonization of the high-latitude regions by immigrants. The first hypothesis postulates an absence of returns to winter-breeding regions and that continuous breeding by remnant populations that survive the summer in low-latitude refugia is responsible for resupplying the high-latitude regions anew each year (the Pied Piper hypothesis). The second hypothesis states that population growth at each end of the migration route resupplies the opposite breeding area in each year (the "return migration" hypothesis).

To distinguish between these hypotheses, we used a national network of light traps (32) to quantify intra- and interannual variation in *A. gamma* populations at ground level during 1976–2009 and specially developed vertical-looking entomological radars (9) to quantify the intensity of high-altitude migrations into and out of the United Kingdom in 2000–2009 (Fig. 1). The radars show that *A. gamma* moths undergo a period of intense northward migration in spring (May and June), followed by greatly reduced randomly orientated flights during midsummer (July), and another period of intense southward migration in the fall (August and September) (Fig. 2, Fig. S1, and Table S1). We therefore restricted analyses of migration intensities to radar data collected during the spring and fall journeys.

Results and Discussion

Summer *A. gamma* populations in the United Kingdom showed a pronounced pattern of annual abundance: during 2000–2009,

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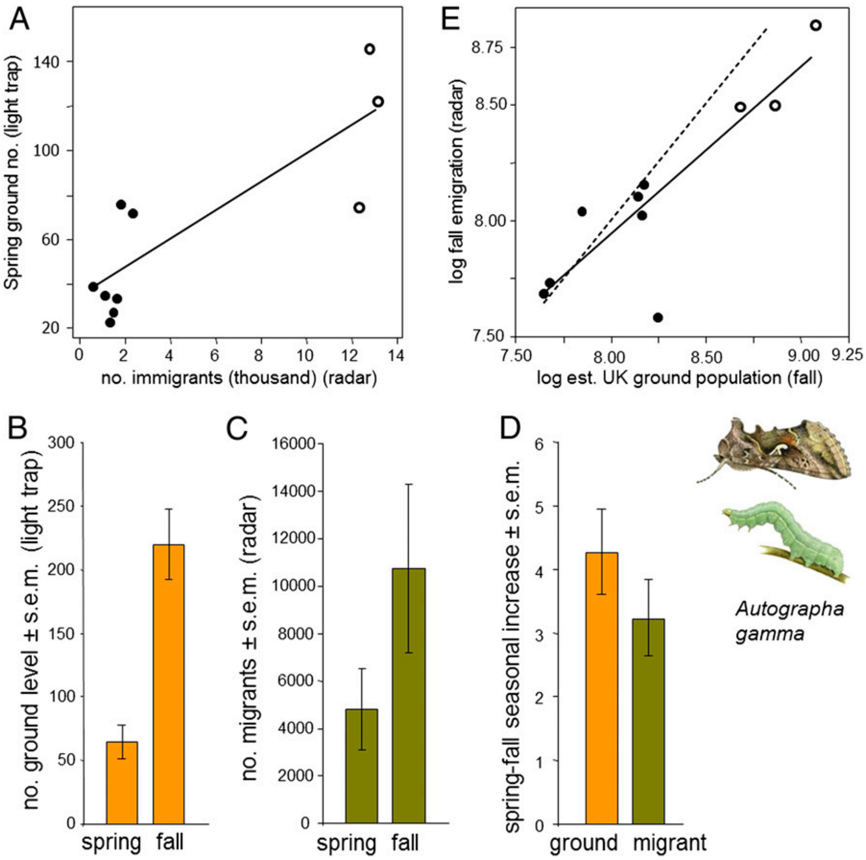

Fig. 1. Seasonal changes in *Autographa gamma* populations and migrations. (*A*) Annual variation in the mean nightly flux per square kilometer of high-altitude spring immigrants to the United Kingdom recorded at two radar stations in 2000–2009 compared with measurements by 25 light traps of the adult spring populations established at ground level. Mass invasions (open circles) occurred in 2000, 2003, and 2006 ($y = 33.78 + 0.00664x$, $n = 10$, $F = 19.11$, $P = 0.002$, $r^2 = 70.5\%$). (*B*–*D*) seasonal changes in the United Kingdom ($n = 10$ y): (*B*) mean number recorded at ground level by light traps in spring and fall (Student's paired $t = -5.6$, $P = 0.000$); (*C*) mean nightly flux per square kilometer of high-altitude spring immigrants and fall emigrants measured by radar ($t = -2.53$, $P = 0.032$); (*D*) mean annual population increases ($t = 1.81$, $P = 0.104$). (*E*) Total number of emigrants that migrated southward measured by radar against the estimated total UK *A. gamma* population each fall (dashed line = 1:1, $y = 2.231 + 0.714x$, $n = 10$, $F = 23.39$, $P = 0.001$, $r^2 = 74.5\%$).

three mass invasion years (2000, 2003, and 2006) had high immigrant migration fluxes in spring—775,000 ± 15,000 moths km^{-2} (mean ± 1 SE), corresponding to an estimated 225–240 million adult *A. gamma* immigrating into the whole United Kingdom—whereas the other 7 y received roughly one-ninth that number: 88,000 ± 12,000 moths km^{-2}, corresponding to ~10–40 million immigrants (Table S2). This variation correlates closely with light-trap monitoring of the size of the population founded at ground level by these immigrants each spring (Fig. 1*A* and Table S3).

In 2000–2009, each moth arriving in the spring (first generation) produced 4.3 ± 0.7 adults in the next (second) UK generation (Fig. 1 *B* and *D*), with similar (mean = 4.8) seasonal increases occurring over all of the 34 consecutive years for which we possess light-trap data (Fig. 3*A*). However, although the second generation is more abundant, it is also less variable than the first (coefficient of variation = 0.595 and 0.906, respectively). This difference is explained by density-dependent mortalities regulating population growth, for which the intercept in Fig. 3*B* indicates a mean summer UK carrying capacity of 340 million adult *A. gamma* during 1976–2009 (calibrated from the mean ratio of annual radar estimates to light-trap counts).

During the fall, radar data showed that emigrant *A. gamma* always left the United Kingdom in higher numbers than had arrived the previous spring, with a mean seasonal increase of 3.2 ± 0.6 individuals for every individual that arrived in spring, similar to the fourfold mean increase estimated from light traps (Fig. 1 *C* and *D* and Tables S2 and S3). Thus, the estimated absolute size of the UK population in the fall—calculated by multiplying the estimated number of spring immigrants each year by the annual increase measured by light traps—was similar to, and closely correlated with, the radar estimates of the total number of moths that emigrated south from the United Kingdom each fall (Fig. 1*E*). With no *A. gamma* surviving over the winter in the United Kingdom (or at similar latitudes across Europe), we conclude that the entire population emigrates annually toward its winter-breeding grounds.

For the apparent reproductive benefits of high-latitude breeding (fourfold population increase) to be realized, moths are dependent upon successful return migrations in the fall. To evaluate these migrations, we used a version of the atmospheric dispersion model "Numerical Atmospheric-dispersion Modeling Environment" (NAME) (*Methods*) that combines the effect of wind currents with *A. gamma* flight behavior [e.g., selection of favorable airstreams and beneficial flight headings (22–25)] to simulate migration pathways of emigrants leaving the United Kingdom on 30 nights when mass return migrations were detected by radar. The model assumes moths took off at dusk from either of two radar sites in southern England and flew for 8 h per night for the first 3 suitable migration nights during a 6-night migration "window" (*Methods*). The mean migration distance (798 ± 47 km; Table S4) and direction (Rayleigh test: mean = 157°, $r = 0.88$, $n = 30$, $P < 0.001$) resulted in ~80% of 3-d trajectories reaching warmer latitudes around the northern fringe of the Mediterranean suitable for the production of the next generation (Fig. 2). We conclude that failure of adults to reach overwintering destinations is low in comparison with the three- to fivefold reproductive benefits accrued by individuals that travel to higher latitudes for summer breeding: We therefore reject the Pied Piper hypothesis and accept the return migration hypothesis.

Remarkably little is known about the biology of *A. gamma* (or most other migrant insects) during winter, but we can predict its dynamics using population-level models (*Methods*) derived from the 34-y time series of spring and fall UK numbers (Fig. 3*A*). We assumed initially that the UK fall population of *A. gamma* equates to the annual founder population on the overwintering sites and vice versa in spring (Fig. S2). On the basis of this

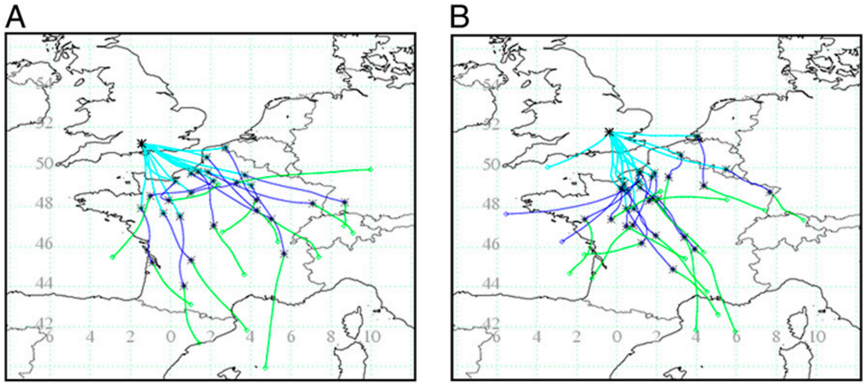

Fig. 2. Simulated nightly fall migration trajectories for adult *Autographa gamma* moths modeled to initiate flight from two radar sites in southern England during August 2003 and 2006. Each colored line is the mean trajectory of 100 simulated moths on a single night, taking off at 2000 hours GMT and flying until 0400 hours GMT (or 0600 hours if over the sea at 0400 hours). Different colors represent successive nights of migration (light blue, first night; dark blue, second night; green, third night) across Western Europe; numbers indicate degrees of longitude and latitude. (*A*) Thirteen migration trajectories in August 2006 from Chilbolton, Hampshire. (*B*) Seventeen migration trajectories in August 2003 and August 2006 from Rothamsted, Hertfordshire.

assumption, our model has the following assumptions: (*i*) Mortality during migration is low (justified above and tested below); (*ii*) the relative numbers of moths emigrating from and recolonizing the United Kingdom are representative of populations elsewhere in Europe, as evinced by similar seasonal population increases over the same time period ~500 km farther north in southern Sweden (mean = 6.1 ± 1.4; Table S5) to those observed in the United Kingdom (Table S3); and (*iii*) winter-breeding grounds do not support resident populations over summer, which is well supported by data from Egypt and Israel (27–29) and our own analysis of light-trap records (30, 33) from Morocco, Egypt, and Israel that show essentially no *A. gamma* during the three summer months (mean population decline between winter and summer of 98% ± 3%, $n = 5$ traps), demonstrating that *A. gamma* effectively vacates its winter-breeding range after spring due to unsuitably hot and/or dry summer climates and a dieback of larval host plants. Making these simple assumptions, we find that the high-latitude summer and low-latitude winter populations of *A. gamma* are regulated by the same linear density-dependent process (Fig. 3 *B* and *C*). However, although the slopes of the relationships of density on net growth rate are the same for the two locations, the intercepts differ, indicating that the carrying capacity of low-latitude populations is only 18% that of high-latitude populations (roughly equating to 60 million moths at low latitude). This is undoubtedly an underestimate, because it excludes losses during migration. Nevertheless, expected values from our Bayesian state-space model (*Methods*) closely match observed UK population sizes when no mortality is assumed during migration (Fig. 3*A*). This result is confirmed through sensitivity analyses where we explore different combinations of loss on each journey and show that high mortalities (>50%) during migration are highly unlikely to describe the observed source-sink dynamics (Fig. 3 *D* and *E*).

Taken together, our findings indicate that *A. gamma*, and possibly other insect migrants, should be reclassified as an obligate migrant whose primary populations inhabit high-latitude temperate zones and are connected with low-latitude winter-breeding sites that represent annual bottlenecks. These results provide an important step toward quantifying the evolutionary drivers of long-range migrations in insects. Understanding the dynamics is also economically important, for *A. gamma* becomes a major pest of many African, Asian, and European crops during outbreak years (26). Just how representative *A. gamma* is of other migrant insects is a matter for future study, but given the similarities in the migration strategies of *A. gamma* to those of other insects in Europe (24, 34), Asia (21), North America (3, 5, 19, 20), and Australia (8, 35), it is very likely that the results of the present study will be applicable to a wide range of migrants. We conjecture, therefore, that during a time when most sedentary Lepidoptera (36, 37) and many migrant birds (38, 39) have experienced dramatic declines, the shared traits of high fecundity (40), polyphagy (26), year-round breeding (26), reduced disease and parasite loads (41, 42), and efficient strategies for the use of windborne transport (43) to exploit widely dispersed seasonal resources are the principal factors that have enabled the recent temperature-related range expansions and population increases observed in many species of migrant Lepidoptera (44). Considering the pest status of *A. gamma* (and many other species of migrant moths), which is facilitated by their polyphagy, it is certainly germane to increase our understanding of the migration systems of such species.

Methods

Radar Observations of *A. gamma* Migrations. We estimated the migratory flux rates of high-flying *A. gamma* moths engaged in spring migration into the United Kingdom and fall (return) migration out of the United Kingdom, using data collected by two purpose-built, vertical-looking entomological radars (VLR) situated in southwest and southeast United Kingdom. The former was at Malvern, Worcestershire [latitude (lat.) 52° 06′ 04′′ N, longitude (long.) 2° 18′ 38′′ W] from 2000 to 2003 and then at Chilbolton, Hampshire (lat. 51° 8′ 40′′ N, long. 1° 26′ 13′′ W) from 2004 to 2009, whereas the latter radar has been at Rothamsted, Harpenden, Hertfordshire (lat. 51° 48′ 32′′ N, long. 0° 21′ 27′′ W) from 1999 onward. The VLR equipment and operating procedures are described in detail elsewhere (9, 45, 46). Briefly, the radars provide a range of information—including body size, flight altitude (insects are detected within 15 separate altitude bands), aerial density, displacement speed, displacement direction, and flight heading—for all individually resolvable insects of > 2 mg body mass that fly through the vertically pointing beam within the altitude range of ~150–1,200 m above the radar site. The VLRs are operated for a 5-min sampling period every 15 min throughout the daily cycle, thus giving a total of 24 sample periods within the 6-h period of nocturnal flight activity (from sunset onward) that we used in this study.

Identification of Radar-Detected *A. gamma* Moths. Aerial netting at 200 m above the ground (22, 24, 47) and captures in 12-m-high suction traps (34) clearly demonstrate that macromoths are the only large (>50 mg) insects that are abundant, high-altitude, nocturnal migrants in the United Kingdom. We can thus be highly confident that the vast majority of VLR-detected large nocturnal insect targets were macromoths, and the aerial composition of this family in the United Kingdom is dominated by *A. gamma* (22–25, 34, 47). Only one other species of noctuid moth has been caught migrating at altitude above the United Kingdom—the large yellow underwing *Noctua pronuba* (47)—but this species has a mean body mass more than twice that of *A. gamma* (34), and so radar returns produced by this species can be easily distinguished from those produced by *A. gamma* during the initial data processing. We identified radar-detected individuals of *A. gamma* by a previously published procedure (22–25), whereby the VLR database of nocturnal insects (flying for 6 h after sunset) was filtered for radar targets that had an estimated body mass falling within the measured range of *A. gamma* [146 mg ± 35 mg (mean ± 1 SD), $n = 11$]. Data on *A. gamma* migration were collected for each year between 2000 and 2009 inclusive, which included three mass invasion years (2000, 2003, and 2006) and seven weak invasion years (Fig. 1).

Estimation of Annual Populations. Year-to-year variation in the annual population abundance of *A. gamma* throughout the United Kingdom was estimated by comparing the mean annual catch from 25 light traps that form part of the Rothamsted Insect Survey national network (32). This network contains ~100 identical light traps across the whole of the United Kingdom

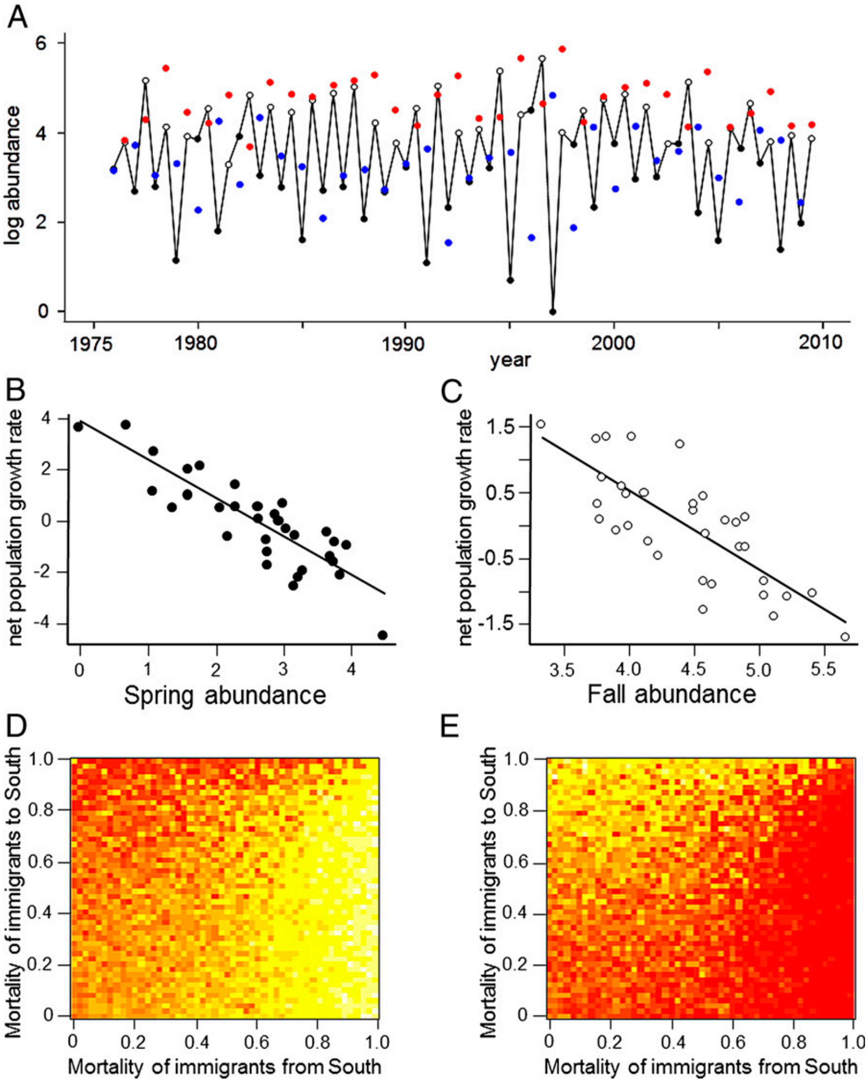

Fig. 3. Population dynamics of *Autographa gamma* 1976–2009. (*A*) Observed spring (solid circles) and fall (open circles) mean numbers at UK light traps that sampled 68 consecutive generations. Colored points indicate abundance before emigration from southern winter-breeding grounds (blue) and the United Kingdom (red) predicted by our Bayesian state-space model, assuming no migratory losses between breeding grounds. (*B* and *C*) Plots of the net growth rate change on a log scale during summer breeding in the United Kingdom (*B*) or winter breeding in Africa and the Mediterranean basin (*C*), in the following year, regressed against log abundance in the current year. If populations are regulated, then it is expected that at high density net growth rate (on a log scale) should be negative (populations decline in size) and conversely at low density net growth should be positive (and populations should increase). The plots and associated analyses show that both populations are regulated by the same density-dependent process (i.e., migration losses in *C* are density independent and/or low): ANCOVA ($n = 32$) shows no significant season-by-density interaction ($F_{1,62} = 1.18$, $P = 0.281$), only season ($F_{1,63} = 91.125$, $P < 0.001$) and density effects ($F_{1,63} = 37.863$, $P < 0.0001$). (*D* and *E*) Sensitivity test of effect of mortalities during migration, shown as the goodness-of-fit of model predictions to observed moth dynamics (*A*), assuming different combinations of loss on both migration journeys: (*D*) fit to UK population; (*E*) fit to African-Mediterranean population, where white-yellow indicates poorer fit, and red indicates best fit based on normalized root mean-square error.

that are emptied on a nightly basis throughout the year. We selected 25 traps that ran continuously from 2000 to 2009, caught reasonable numbers of *A. gamma* (mean of 16.4 ± 0.9/y), and provided reasonable geographical coverage of the United Kingdom, although they were concentrated mostly in the south (mean latitude = 52.3665° N; Fig. S3). The mean annual catch from these 25 traps was used as a proxy for the abundance of the total UK population and compared directly with the radar counts. Seasonal increases in population abundance (Table S3) were calculated by dividing the total catch across the 25 light traps during "fall" (August and September) by the total catch during "spring" (May and June). In addition, we selected 12 light traps that had caught good numbers each year and been run continuously since 1976 to derive the long-term (34-y) dynamics and analyses shown in Fig. 3. Data on adult *A. gamma* seasonal abundance, obtained from volunteer-run light traps (between 20 and 120 traps per year) in southern Sweden (data stored on the Swedish Species Gateway website, www.artportalen.se), were analyzed for comparative purposes. These traps had a mean geographical location ~500 km farther north than the mean position of the UK traps (mean latitude = 57.6966° N; Fig. S4 and Table S5).

Trajectory Analyses. We modeled the fall return migration trajectories of *A. gamma* moths into Europe over 3 consecutive migration nights during 30 separate occasions when mass migrations of this species were recorded by the VLRs, leaving southern England during August 2003 and August 2006. Simulated nightly trajectories were produced by running a specially modified version of the Met Office dispersion model NAME that has *A. gamma* flight behavior incorporated (24). NAME is a Lagrangian atmospheric dispersion model that is more typically used to predict the forward trajectories of passively advected gases and sedimenting particles, but that has also been used to simulate the migrations of the midge vectors of bluetongue (48). The modifications used here are described in full elsewhere (24). When simulating moth trajectories on the first night of migration, we assume that the moths are carried by the wind and are gradually dispersed in the horizontal by atmospheric turbulence, but counteract this to some extent by seeking to fly toward a preferred direction. The active flight behavior is represented by a constant air speed of 5 $m \cdot s^{-1}$ in addition to the local wind velocity, toward the mean heading of *A. gamma* moths (as measured by the VLR) during each particular mass migration event. By combining this velocity with the local flow, using the mean wind and turbulence fields from the simulation model, their flight trajectory is calculated (24). *A. gamma* moths also actively select fast, high-altitude winds (22–25). To represent this flight behavior, the modeled moths were all released at the height of the fastest winds in the boundary layer coincident with the release time and location of each trial and constrained to fly at this altitude for the duration of the simulation. Groups of 100 moths were released from either the Rothamsted radar site ($n = 17$ nights) or the Chilbolton radar site ($n = 13$ nights), and their displacement pathways were simulated by the model. Trajectories showing the chronological sequence of positions of the mean value of the 100 moths at each time step (10 min) were plotted from the release location and time [2000 hours Greenwich mean time (GMT)] for a flight duration of 8 h or for 10 h if the moths were still over the sea at 0400 hours GMT (Fig. 2).

After landing, the modeled moths were retained at the same location throughout the following day, until they chose whether to migrate again (or not) at 2000 hours the following evening. Moths undertook their second night's migration if the local wind direction at 2000 hours at the flight altitude (the height with the fastest winds in the nocturnal boundary layer) was broadly favorable (i.e., blowing toward an approximately southward direction, between 100° and 260°). If the wind at flight altitude was not blowing toward this sector at 2000 hours, the moths did not migrate and remained at the location overnight. This process was repeated, until the moths either were exposed to a favorable wind direction (as defined above) or had not migrated on the 2 previous consecutive nights, when they would undertake their second night's migration irrespective of the wind direction. The same methodology was used to simulate the third (final) migration night, which occurred within 5 d of the first night in all 30 cases. The heading direction that the modeled moths were given had to be estimated for the second and third migration nights, as unlike for the first migration night, VLR measurements of actual moth headings were not available. The estimated headings were calculated from the relationship between the wind direction and the flight heading of radar-detected *A. gamma* moths during a large sample (n = 86 nights) of fall mass migration events (Fig. S5).

The overall mean distance and direction of the combined 3 nights of migration trajectories were calculated for each of the two radar sites. In addition, we also calculated the same variables for the trajectories that did not include moth flight behavior (i.e., trajectories that modeled the movement of passively transported inert particles), so that the effect of active, oriented flight behavior over the 3 nights of migration could be ascertained (Table S4).

Data Analysis. Seasonal population abundances, seasonal migration intensities, and seasonal increases in these two parameters were all log-transformed before analysis with paired t tests and linear regression.

Calculation of Radar-Measured Migration Intensities. We calculated an aerial density value (per 10^7 m^3) for each individual *A. gamma* moth detected by the radars, on the basis of the volume of atmosphere sensed by the VLR and the displacement speed of each individual moth (45). The total aerial density of migrating *A. gamma* above each radar site on each night during the spring and fall migration seasons in each of the 10 y was calculated in the following manner. First, we summed the aerial-density values of all of the individual moths detected during each 6-h nocturnal flight period and then divided this value by 24 (the number of radar-sampling periods) and by 15 (the number of altitude bands within which moths were recorded). This value (X) is equal to the total aerial density of *A. gamma* per 10^7 m^3 on each night within the air column above the radar site. We converted these aerial-density values to nightly migration-flux values through a 1 × 1-km (10^6 m^2) window above the radar, running west to east [and thus parallel to the principal migration directions during the spring and fall (22–25)]. This conversion was achieved by the following procedure. First, the flux through the 1-km^2 window each second (Y) was calculated by Y (km^{-2}·s^{-1}) = (X/10) × mean displacement speed (m·s^{-1}). Second, the total migration flux through the 1-km^2 window over the 6-h nocturnal flight period (Z) was calculated by Z (km^{-2}·night^{-1}) = $Y \times 21{,}600$ s. The total migration-flux values km^{-2}·night^{-1} (Z, Fig. S1) were used to calculate the mean nightly flux rate of moths during the whole of the spring and fall migration seasons, for each year and across both radar sites (Table S2). To calculate the total seasonal immigration to the whole United Kingdom, we extrapolated from the nightly flux rates above each radar site to produce an estimate of the numbers crossing a line running parallel to the main migration direction (west to east) along a 300-km stretch of the UK south coast (Table S2). These will be conservative estimates, as the southern English coastline is considerably longer than 300 km (~520 km in a straight line from the western extremity to the eastern extremity).

Analysis of Directional Information. The VLRs automatically record the displacement direction of each individual insect as it passes through the beam overhead. Using the Rayleigh test of uniformity for circular data (49), a number of parameters relating to the mean displacement direction (i.e., the migration direction) were calculated for all mass migration "events" during the three mass invasion years (2000, 2003, and 2006). A migration event is defined as all of the individual nights that compose 90% of the cumulative seasonal (spring, summer, and fall) total of the individual radar-detected *A. gamma* moths (25). For each event, the Rayleigh test was used to calculate the mean displacement direction, the mean resultant length r (a measure of the clustering of the angular distribution ranging from 0 to 1, with higher values indicating a greater degree of clustering) for each distribution, and the probability that these distributions differed from uniform (a P value <0.05 indicates that the distribution is significantly unimodal and hence the individual insects demonstrate a significant degree of common alignment of their displacements).

We then calculated the overall mean migration direction of all *A. gamma* mass migration events in the three mass invasion years for each successive 2-wk period from early May until late September, by analyzing the individual nightly mean displacement directions with the Rayleigh test once again. If the distribution of nightly mean displacement directions was also significantly unimodal, we assumed that there was a significant preferred migration direction during this period. The results indicated that there were significant common migration directions toward the north in all four 2-wk periods during spring (May and June) and toward the south in all four 2-wk periods in the fall (August and September), but that there was no overall pattern of preferred movement during either of the 2-wk periods in midsummer (July) (Table S1).

Models and Analysis of Population Dynamics. The *A. gamma* populations are represented by two sets of dynamics: a spring population (representing migrants arriving from the low latitude winter-breeding zone) and a fall population (representing emigrants leaving the United Kingdom) (Fig. S2). Two statistical analyses were used to explore its dynamics from 1976 to 2009, using UK moth-trap counts and initially assuming full migration of populations between each region and no losses (predation, failure to reach breeding grounds) *en route* (see Fig. 2 and main text for justification). First, we explored the general patterns in the observed counts, using an analysis based on (log) changes in population size from one year to the next and log (density). The hypothesis is that the population is regulated through temporal density dependence with the prediction being that the relationship between this net population growth rate analysis and density is negative. The second analysis used a hierarchical Bayesian state-space approach to link the observed counts to the expected dynamics. Building on the known natural history of *A. gamma* and the analysis on net growth rate, an appropriate population model is proposed to describe the expected dynamics. We link the observed and expected dynamics by accounting for the error in measuring populations precisely. A schematic of this is shown Fig. S2.

To link the counts to the dynamics we assume that measurement error is Poisson distributed,

$$D_{n_t} = \mathrm{Poisson}(n_t) \qquad [1]$$

$$D_{m_t} = \mathrm{Poisson}(m_t), \qquad [2]$$

where D_{n_t} and D_{m_t} are the counts from Spring and Fall light traps in the United Kingdom. This assumption leads to the discrete-time model

$$n_t = d(m_{t-1}) + \lambda_n n_{t-1} f(n_{t-1}) \qquad [3]$$

and

$$m_t = d(n_{t-1}) + \lambda_m m_{t-1} f(m_{t-1}), \qquad [4]$$

where n_t and m_t are expected population sizes, and λ_n and λ_m the intrinsic growth rates, respectively at time t in the United Kingdom and the "south"; $d(m_{t-1})$ and $d(n_{t-1})$ describe migration from low-latitude breeding sites to the United Kingdom and vice versa; and $f(n_{t-1})$ and $f(m_{t-1})$ describe density dependence in each breeding ground. This process leads to a discrete model for Bayesian time-series analysis,

$$n_t = m_{t-1}\exp(-\gamma_m m_{t-1}) + \lambda_n n_{t-1}\exp(-\alpha n_{t-1}^{\beta}) \qquad [5]$$

and

$$m_t = n_{t-1}\exp(-\gamma_n n_{t-1}) + \lambda_m m_{t-1}\exp(-\alpha m_{t-1}^{\beta}), \qquad [6]$$

which includes parameters associated with density dependence (α, β) and the dispersal function for immigrants founding spring (γ_m) and fall (γ_n) populations. Analysis of Eqs. **1** and **2** detects the existence, strength, and nature of any density-dependent processes affecting populations in the United Kingdom and in the winter breeding grounds (Fig. 3 *B* and *C*), whereas Eqs. **5** and **6** generate the predicted sizes of *A. gamma*'s populations in its northern and southern zones for 68 consecutive generations, initially assuming successful full migrations in each direction every year (Fig. 3*A*).

Sensitivity tests were carried out on the goodness-of-fit of Eqs. **5** and **6** to the observed populations of *A. gamma* in the United Kingdom (Fig. 3*A*), assuming different combinations of adult moth loss during each migration on each population. We do this test by including an additional mortality term on the founding immigrants associated with the spring and fall populations,

$$n_t = (1-\mu_m)m_{t-1}\exp(-\gamma_m m_{t-1}) + \lambda_n n_{t-1}\exp(-\alpha n_{t-1}^{\beta}) \qquad [7]$$

and

$$m_t = (1-\mu_n)n_{t-1}exp(-\gamma_n n_{t-1}) + \lambda_m m_{t-1}exp(-\alpha m_{t-1}^{\beta}), \qquad [8]$$

where μ_m and μ_n are mortalities acting on the spring and fall migrants, respectively. We refitted this model (Eqs. **7** and **8**) with fixed different combinations of mortalities to the observed time series, using our Bayesian state-space approach (outlined above). We evaluate the difference between observed and predicted moth counts using normalized root mean-square error such that lower values indicate less residual variance and hence better fit to data.

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