

Wind Selection and Drift Compensation Optimize Migratory Pathways in a High-Flying Moth

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Summary

Numerous insect species undertake regular seasonal migrations in order to exploit temporary breeding habitats [1]. These migrations are often achieved by high-altitude wind-borne movement at night [2–6], facilitating rapid long-distance transport, but seemingly at the cost of frequent displacement in highly disadvantageous directions (the so-called “pied piper” phenomenon [7]). This has led to uncertainty about the mechanisms migrant insects use to control their migratory directions [8, 9]. Here we show that, far from being at the mercy of the wind, nocturnal moths have unexpectedly complex behavioral mechanisms that guide their migratory flight paths in seasonally-favorable directions. Using entomological radar, we demonstrate that free-flying individuals of the migratory noctuid moth *Autographa gamma* actively select fast, high-altitude airstreams moving in a direction that is highly beneficial for their autumn migration. They also exhibit common orientation close to the downwind direction, thus maximizing the rectilinear distance traveled. Most unexpectedly, we find that when winds are not closely aligned with the moth’s preferred heading (toward the SSW), they compensate for cross-wind drift, thus increasing the probability of reaching their overwintering range. We conclude that nocturnally migrating moths use a compass and an inherited preferred direction to optimize their migratory track.

Results and Discussion

In contrast to well-known, long-distance, day-migratory butterflies such as the Monarch [10], nocturnal migrant moths have only a short migration “window,” because migratory flight is limited to just a few nights following adult emergence

and before adult reproductive maturity [11]. Furthermore, the flying (air) speeds of moths are only $\sim 5 \text{ ms}^{-1}$, so how they are able to achieve “goal-oriented,” long-distance migrations in seasonally-advantageous directions has remained an enigma [8, 9]. To solve this problem, we studied the silver Y moth, *Autographa gamma* (Lepidoptera: Noctuidae), a noted migrant and an economically important agricultural pest species [12]. Like many other insect migrants, *A. gamma* arrives in the UK during spring and breeds through several generations over the summer before returning south to overwintering sites in the Mediterranean region in the autumn [11].

We investigated the return migration of *A. gamma* in the UK during August 2000 and August 2003 when the species was particularly abundant (Figure S1, available online). We used a specially developed vertical-looking entomological radar [13], which enabled us to examine the nocturnal flight behavior of *A. gamma* during 42 mass-migration “events” (see **Experimental Procedures**, “Selection of Migration Events”) at high altitudes ($> 150 \text{ m}$ above ground level [AGL]). During these mass-migration events, the moths tended to concentrate at the altitude of maximum wind speed (linear regression, $r^2_{\text{adj}} = 0.23$, $F_{1, 20} = 7.3$, $p < 0.05$, Figure S2), whereas there was no relationship between the height of predominant moth migration and the height of the temperature maximum (linear regression, $r^2_{\text{adj}} = 0.02$, $F_{1, 20} = 1.4$, $p = 0.26$). This was unexpected, given that in northern temperate regions, nocturnal layers of insects are usually constrained to fly at the altitude of the warmest airstreams [14, 15]. Thus, *A. gamma* moths are able to select the fastest airstreams to maximize their displacement speed and migration distance.

More than 90% (38/42) of the mass-migration events of *A. gamma* occurred on nights with northerly winds, so the mean-displacement direction of the moths was approximately southwards (Rayleigh test, mean displacement = 202° , $R = 0.58$, $p < 0.001$, $n = 42$, Figure 1A). This highly directed distribution of moth displacements during the mass-migration events contrasted strongly with that of the nocturnal, high-altitude winds over the study period, which blew from all compass directions with almost equal frequency and did not differ from a random distribution (Rayleigh test, mean direction = 297° , $R = 0.12$, $p = 0.15$, $n = 121$, Figure 1B). Thus, *A. gamma* maintained flight at high altitudes only on those nights with winds favorable for return migration to overwintering areas. Our analysis of meteorological variables did not reveal any factors (such as temperature, humidity, wind speed, wind direction, or atmospheric pressure) that might have allowed migrants at ground level to select suitable high-altitude winds (see **Supplemental Data**, “Meteorological Analyses”), so we presume that moths routinely take off at dusk and climb to altitude but descend again if they find themselves being displaced in the wrong direction. This mechanism for selection of suitable winds requires the use of a compass during flight at high altitudes, but as yet no nocturnally migrating insect has been convincingly shown to have such a compass sense. So, do nocturnally migrating moths possess such a compass?

Migrant insects must actively fly to keep themselves aloft in the fast-moving favorable airstreams [16]. If high-flying *A. gamma* have a compass sense, one would predict that

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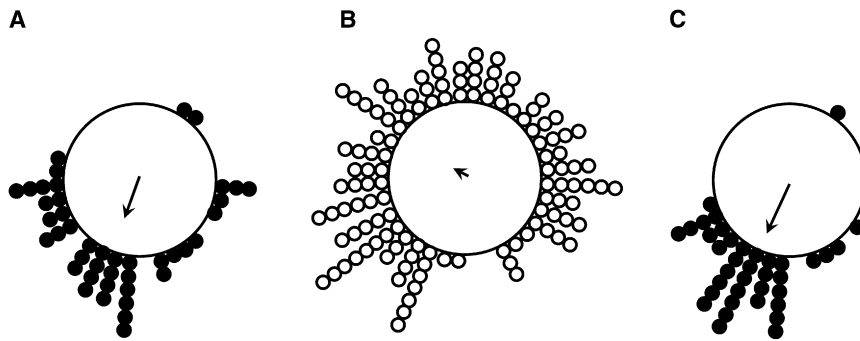


Figure 1. Circular Distributions of Directional Data Obtained during Return Migrations of *Autographa gamma*

Mean directions from each event are plotted (small circles at periphery). The bearing of the solid black arrow indicates the mean direction of the dataset, and the length of the arrow is proportional to the clustering of the dataset about the mean.

(A) The mean tracks of high-flying migrant *A. gamma* during the 42 mass-migration events detected by vertical-looking radar (mean direction = 202°).

(B) The wind direction at 300 m at both radar sites during the migration periods.

(C) The mean flight headings of migrant *A. gamma* during the 37 events with significant common orientation (mean heading = 205°).

they would actively contribute to their wind-driven southwards movement by also heading in their migratory direction. Therefore, we examined the distributions of their flight headings during mass-migration events. In 88% (37/42) of the mass-migratory events during this period, the migrant moths showed a significant degree of common orientation [17, 18]; i.e., in any one event, the moths' headings were centered about a common direction (Figure S4). Considering these 37 events, 36 had a mean heading that was southwards, with an overall mean direction toward SSW (Rayleigh test, mean heading = 205°, $R = 0.83$, $p < 0.001$, $n = 37$, Figure 1C). The mean heading of all individual radar-detected *A. gamma* throughout the study period (not just those in the mass-migration events) was identical (Rayleigh test, mean heading = 205°, $R = 0.31$, $p < 0.001$, $n = 4495$). We therefore conclude that the overall mean heading of 205° recorded in the present study represents the inherited migratory direction of second-generation UK populations of *A. gamma* (hereafter referred to as the presumed inherited direction, PID). The mean-heading and mean-track directions were very similar (only 3° different); thus, the migrants would have added their airspeed of $\sim 5 \text{ ms}^{-1}$ to the wind speed, greatly increasing their migration distance. However, the moths could theoretically improve their directedness even further if they adopted headings that would bias their windborne displacements toward their PID. So, are nocturnally migrating moths capable of compensating for crosswind drift? To answer this question, we examined the magnitude of the difference between the moths' heading and track, here called the correction angle (see Supplemental Data, "Correction and Deviation Angles" and Figure S5), for each mass-migration event.

During mass-migration events when the drift angle (the difference between the track and the PID [19]) was large ($> 20^\circ$), the mean-correction angle was $+27^\circ$, which was highly significantly different from zero ($p < 0.01$, since the 99% confidence intervals $[\pm 10^\circ]$ did not include 0° ; $n = 22$). Furthermore, the correction was always in the expected direction, i.e., toward the PID (Figure 2). However, for the events where the drift angle was small ($< 20^\circ$), the mean-correction angle was $+5^\circ$, and only nine of the 14 cases were toward the PID (Figure 2). The correction angle in this case was not significantly different from zero ($p > 0.05$ as the 95% confidence intervals $(\pm 5^\circ)$ included 0° ; $n = 14$). Thus the moths only compensated significantly for crosswind drift when the drift angle exceeded 20° . Further analysis demonstrated that larger correction angles produced correspondingly larger deviations of the track away from the downwind direction and toward the PID (Figure 3). This result proves that the moths partially compensated for crosswind drift, so that the resultant tracks were closer to the preferred

direction than they would have been had the moths simply flown downwind. The combination of behavioral mechanisms described here enabled the moths to migrate up to 650 km per night in a seasonally advantageous direction (see Supplemental Data, "Flight Duration and Migration Distance"). Low-flying diurnal migratory butterflies and dragonflies are known to compensate for crosswind drift [20, 21], as do foraging bumblebees and honey bees [22, 23], but our results are the first

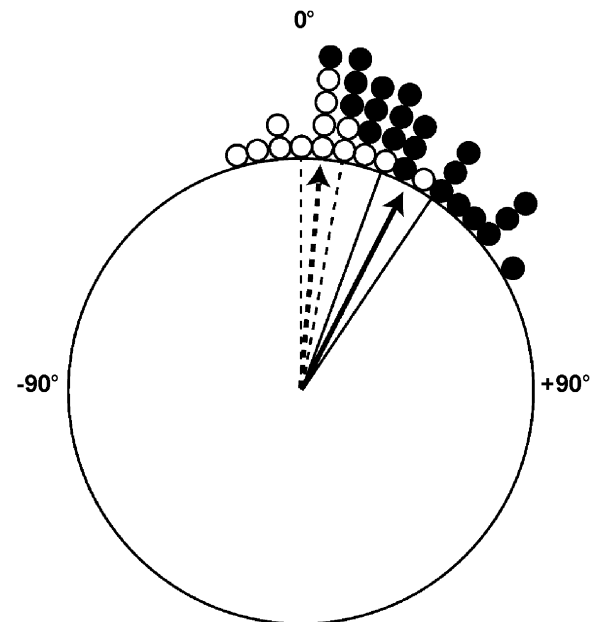


Figure 2. Mean Correction Angles of Migrating *Autographa gamma*

A correction angle (circles at periphery) of 0° indicates that the mean heading of the moths was identical to the mean-displacement direction on that particular night. Positive values (clockwise from 0°) indicate that the moths compensated for wind drift by heading in a direction further toward the presumed inherited migration direction (PID = 205°) than their current displacement direction. Conversely, negative values (counterclockwise from 0°) indicated orientation away from the PID. Filled circles: events where the mean-displacement direction of the moths differed $> 20^\circ$ from the PID. Open circles: events where displacement differed $< 20^\circ$ from the PID. Solid arrow and lines: sample mean vector (correction angle = $+27^\circ$, $R = 0.96$, $n = 25$) for the solid circles and its 95% confidence intervals. Dashed arrow and lines: sample-mean vector (correction angle = $+5^\circ$, $R = 0.98$, $n = 14$) for the open circles and 95% confidence intervals. The figure shows that *A. gamma* moths compensate for wind drift when their displacement directions are $> 20^\circ$ from their preferred migratory direction but not when they are $< 20^\circ$.

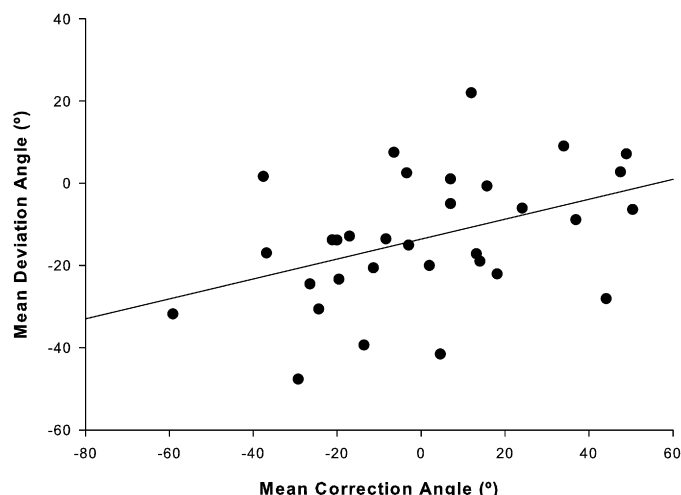


Figure 3. Regression of Moth Deviation Angles and Correction Angles
Positive angles are clockwise (i.e., toward the west of south), whereas negative angles are counterclockwise (i.e., toward the east of south). The data thus indicate that correction angles toward the west actually caused significant deviations in the displacement direction toward the west, producing a displacement closer to the PID of 205° than would have occurred because of wind alone. Likewise, compensatory orientation toward the east also produced displacements closer to the PID.

demonstration of crosswind drift compensation in a high-flying insect migrant. To achieve this feat, the migrant moths must have a compass sense.

The compass mechanism employed by *A. gamma* is unknown. We can rule out a lunar compass, because the moon was below the horizon during one-third of the mass-migration events and very likely would have been obscured by cloud on additional nights. A stellar compass is also highly unlikely, considering the resolution of moth compound eyes [24], whereas a solar compass cannot be the mechanism used by *A. gamma* when flying throughout the night. Thus, a geomagnetic compass is the most likely mechanism, perhaps calibrated at sunset by a solar compass similar to that of nocturnal migratory songbirds [25, 26].

Taken together, our results show that nocturnal migratory moths have evolved a suite of behaviors to facilitate successful migrations to temporary breeding and overwintering areas. The mean-heading and mean-track directions in the current study would be highly adaptive for migrants leaving northern Europe en route to the Mediterranean Basin and are very similar to those of migrant songbirds leaving Sweden in the autumn [27]. The *A. gamma* return migrations were enormous: more than 200 million moths migrated southward across a 150-km-long line across southern Britain in August 2003 (see Supplemental Data, "Migration Flux"). Considering the distances these moths would have flown and their sophisticated orientation behaviors, it is apparent that many will have reached their overwintering regions in just a few nights. These results illustrate how nocturnal insects can migrate in seasonally-advantageous directions even though they are reliant on windborne movement to travel the distances required, and we suggest that these mechanisms might prove to be widespread among large windborne insect migrants. Considering the widespread pest status of many insect migrants and the positive effects of global warming on the frequency of insect migration [28], the long-range movements of such pests will have increasing impacts on global agriculture, and therefore our ability to understand and predict their spatial dynamics will become progressively more important.

Experimental Procedures

Vertical-Looking-Radar Operating Procedures

We studied the flight behavior of high-flying *A. gamma* engaged in return migration with the use of data collected by two vertical-looking radars

(VLR) situated in inland southern England at Harpenden, Hertfordshire (lat. 51° 48' 32" N, long. 0° 21' 27" W) and Malvern, Worcestershire (lat. 52° 06' 04" N, long. 2° 18' 38" W) [13, 29]. Targets flying in a given altitude range above the radar (150 m to 1188 m) are interrogated when they pass through the vertically pointing beam within 15 different height bands. Individual targets can be detected simultaneously in each 45-m-deep height band. Data were collected for a 5 min period in every 15 min, and the returned signals were automatically analyzed with an iterative procedure based on components of their complex Fourier transformations [30]. Usually, the majority of signals are resolved, and the analysis procedure yields the horizontal speed, displacement direction, body alignment, and three radar-scattering parameters of the target. The extracted parameters are then used to create a simulated signal, and the correlation between the simulation and the actual radar return provides a quantitative estimate of how well the parameter-extraction routine has worked [30]. A high correlation coefficient (> 0.9) shows that the measured signal is very well-described by the underlying analysis model and that the estimated characteristics (e.g., displacement vectors and alignments) will be reliable. Targets with a correlation coefficient < 0.9 fit the analysis model less well and are mainly caused by the presence of more than one insect within the same height band at the same time; i.e., interference between insect targets. In this study, we have restricted our analyses to insect targets whose returned signals have correlation coefficients > 0.9, so we can be confident that the extracted flight parameters have been reliably estimated.

Identification of Radar-Detected *A. gamma*

Aerial netting at 200 m above ground demonstrated that during the study period, *A. gamma* was present at high altitudes in much greater abundance than was any other species of moth (see Supplemental Data, "Selection of Study Period"). This was not surprising, considering that it is the only non-overwintering obligate migrant noctuid species that is highly abundant in the UK and that it migrates predominantly during August (Figure S1B). Furthermore, noctuid moths are the only group of large insects (those of > 100 mg body mass) caught at night at high altitudes over the UK [31]. It should be noted that no other insects of *A. gamma* size were caught by aerial netting during the August 2003 study period—those of the nearest size were one or two green lacewings that weighed about 8 mg compared with the ~150 mg mass of *A. gamma*. The only other insect species present at the time were a few tiny flies and aphids, which are not individually detectable by the radar. There were, therefore, no other insects anything like *A. gamma* that the radar algorithms could have confused with that species. Taken together, these factors make it highly likely that the majority of large insects flying at high-altitudes over southern Britain during the study period would be *A. gamma*, so VLR-detected insects relating to this species were identified by a two-stage procedure. First, the body masses of 11 freshly-caught *A. gamma* were measured. The mean \pm 1 standard deviation (146 mg \pm 35 mg) was used to select the mass range (111–181 mg) of VLR-detected insects that were likely to be *A. gamma*. In the second stage of the procedure, the VLR database of nocturnal insects (flying between 20:00 and 24:00 GMT) detected throughout the month of August in 2000 and 2003 was filtered for radar targets that had an estimated body mass falling within the selected mass range.

To confirm that peaks of VLR-detected putative *A. gamma* corresponded to nights when *A. gamma* was abundant, we examined the relationship between the nightly variation in VLR-detected abundance and catches from a national network of light traps during August 2003. The relationship between the Rothamsted VLR data and the mean nightly catch from 12 eastern light traps near Rothamsted was positive and highly significant (linear regression, $r^2_{\text{adj}} = 0.43$, $F_{1, 29} = 24.1$, $p < 0.001$). Similarly, there was a highly significant relationship between the Malvern VLR data and the mean catch from 14 western traps near Malvern (linear regression, $r^2_{\text{adj}} = 0.36$, $F_{1, 29} = 18.0$, $p < 0.001$). Further evidence that one species (*A. gamma*)

predominated in the radar data is provided by the fact that the nightly distributions of flight headings were all unimodal with a tight angular dispersion around the mean heading: the mean circular standard deviation of all 37 migration events was only $32.9^\circ \pm 1.0^\circ$ (mean ± 1 SE). These data support the conclusion that the majority of the VLR-detected insects selected for this study were indeed correctly identified as *A. gamma*.

Selection of Migration Events for Further Study

The combination of two VLR sites and 31 nights in the month of August meant that over the two study years there were 124 date/site combinations (termed "events") for study. The numbers detected by either VLR varied greatly from night to night, from zero to a maximum of 810 individual moths recorded on a single night. Notwithstanding this great nightly variation, the densities of moths detected at the two VLR sites on the same night were significantly positively correlated (linear regression, $r^2_{adj} = 0.30$, $F_{1, 60} = 27.6$, $p < 0.001$), indicating that large migration events occurred simultaneously at the two widely separated locations. The majority of the high-flying *A. gamma* were detected on relatively few nights of major migration activity: two-thirds of the moths (9877 from a total of 14,907) were detected during just one-third of the possible migration events (42 from a total of 124). These 42 mass-migration events were selected for study of the behavior of *A. gamma* engaged in migratory flights.

Calculation of Displacement Directions

The VLR automatically records the displacement direction of each individual insect as it passes through the beam overhead. Wind direction changes with height, and because insect displacement direction is largely controlled by the wind direction, it will also change with height. For the enabling of accurate measurement of the mean-displacement directions of the majority of the migrant *A. gamma*, analysis was restricted to the lowest three radar height bands, 150 m–337 m above ground level, because this was the height range where the greatest densities were recorded. A number of parameters were calculated for each migration event: the mean-displacement direction, the mean resultant length "R" (a measure of the clustering of the angular distribution ranging from 0 to 1), and the probability that this distribution differed from uniform (with the Rayleigh test of uniformity for circular data [32]). An overall mean displacement during the mass-migration events was calculated with the use of data from just these 42 events, and an overall mean from all 4495 *A. gamma* detected in height bands one to three throughout all 124 potential events was also calculated.

Calculation of Orientation Directions

Every insect's body orientation is routinely recorded by the VLR, and this figure corresponds to the flight heading, which might be similar to, or quite different from, the insect's displacement direction. Strictly speaking, the radar measures alignment rather than orientation per se, so there is initially a 180° ambiguity in the heading data [18, 29]. The body-alignment data is analyzed with the double-angles method, but the 180° ambiguity remains [32]. To eliminate this ambiguity in heading direction, we compared the displacement speeds of individual *A. gamma* measured by the VLR with the wind speed at flight height, and we found that displacements were on average about 5 ms^{-1} faster than wind speeds. This difference is of the order expected for the flight speed of *A. gamma* [15] and thus demonstrates that the flight headings were always in the direction closest to the displacement directions (and thus more or less downwind). If the distribution of flight headings recorded during any one event was significantly different from a uniform distribution and strongly clustered (with a high R value), then the moths were designated as exhibiting common orientation [17, 18]—that is, they were all heading in approximately the same direction (Figure S4).

Supplemental Data

Supplemental experimental procedures and five figures are available online at <http://www.current-biology.com/cgi/content/full/18/7/514/DC1/>.

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