

A seasonal switch in compass orientation in a high-flying migrant moth

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Most individual insect migrants have only a short time ‘window’ for migration (just a few nights) and comparatively slow airspeeds. Thus, to achieve long-range displacement into temporary breeding habitats, migrants must hitch a ride on fast-moving, high-altitude winds [1]. We recently demonstrated that the migratory noctuid moth *Autographa gamma* has evolved a compass mechanism which facilitates the successful return of autumn migrants from the United Kingdom to their winter ranges further south via the selection of favourable high-altitude winds [2]; this was the first convincing evidence of such a mechanism in insects that migrate predominantly at high altitudes. As pointed out in a commentary on that work [3], the question of whether or not a similar mechanism promotes northwards migration of such insects during the spring remained unanswered — we do not know if there is a reversal of the migrants’ preferred compass orientation according to season. Here, studying *A. gamma* once again, we report the first evidence that a nocturnal migrant moth controls the direction of both its spring (‘forward’) and autumn (‘return’) high-altitude migrations, and that it also optimises its flight-altitude and compensates for cross-wind drift in a similar manner in both directions.

We studied the high-altitude spring immigrations of *A. gamma* into the southern UK using vertical-looking entomological radars [4]. Spring immigrations are most frequent during the month of June, and we identified 83 high-altitude mass migration ‘events’ between 200 and 1200 m above the radar sites during June of 2000, 2003 and 2006

(see [2] for detailed experimental procedures). As in autumn [2], the maximum aerial density of migrant *A. gamma* in spring usually occurred at considerable heights (mean = 650 m), and migrants tended to concentrate at the altitude of the fastest winds rather than where air temperatures were warmest (linear regressions, $r^2_{adj} = 0.15$, $F_{1,38} = 7.9$, $P = 0.008$ for wind speed; $r^2_{adj} = 0.05$, $F_{1,38} = 3.1$, $P = 0.088$ for temperature).

As expected, the great majority of the 83 mass migration events (94%) occurred on nights when high-altitude southerly winds produced northwards displacements — between 270° and 90° (Figure 1A). The mean displacement direction of all *A. gamma* individuals during the study period was almost directly due north (Rayleigh test, mean

displacement = 354°, $R = 0.66$, $P < 0.001$, $n = 23,338$). By contrast, the equivalent direction of all individual moths during the autumn migrations was 202° [2], and thus the mean displacement direction of the moths switched by ~150° between spring and autumn (Figure 1D). Winds at 300 m during the spring migration periods were predominantly from the south (Rayleigh test, mean direction = 197°, $R = 0.29$, $P < 0.001$, $n = 108$), although winds from non-favourable directions were also frequent (Figure 1B), showing that the ability to select favourable winds is advantageous to migrant moths in both spring and autumn.

During 78 of the 83 spring mass migration events (94%), the high-flying *A. gamma* showed a significant degree of common orientation — in each event, the moths’ individual

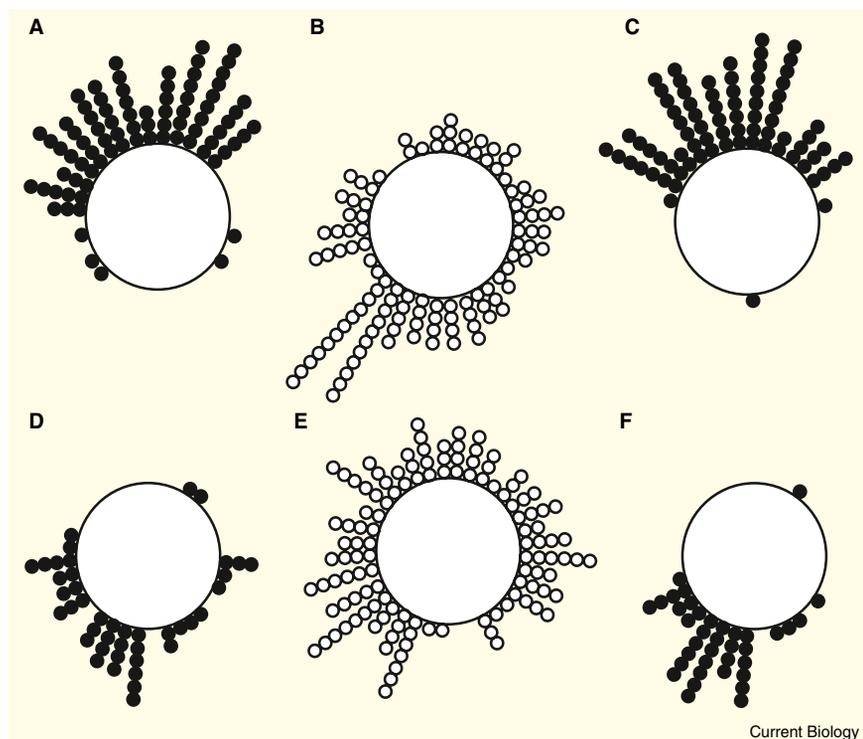


Figure 1. Circular distributions of directional data obtained during high-altitude migrations of *Autographa gamma* over the UK.

Mean directions of each event are plotted (small circles at periphery). (A) The mean displacement directions of high-flying migrant *A. gamma* during the 83 spring mass migration events detected by vertical-looking radar (mean direction of all individuals = 354°). (B) The wind direction at 300 m at both radar sites during the spring migration periods (mean = 197°). (C) The mean flight headings of migrant *A. gamma* during the 78 spring mass migration events with significant common orientation (mean heading of all individuals = 18°). (D) The mean displacement directions of migrant *A. gamma* during the 42 autumn mass migration events analysed in [2] (mean direction of all individuals = 202°). (E) The wind direction at 300 m at both radar sites during the autumn migration periods (mean = 297°). (F) The mean flight headings of migrant *A. gamma* during the 37 autumn mass migration events with significant common orientation analysed in [2] (mean heading of all individuals = 205°).

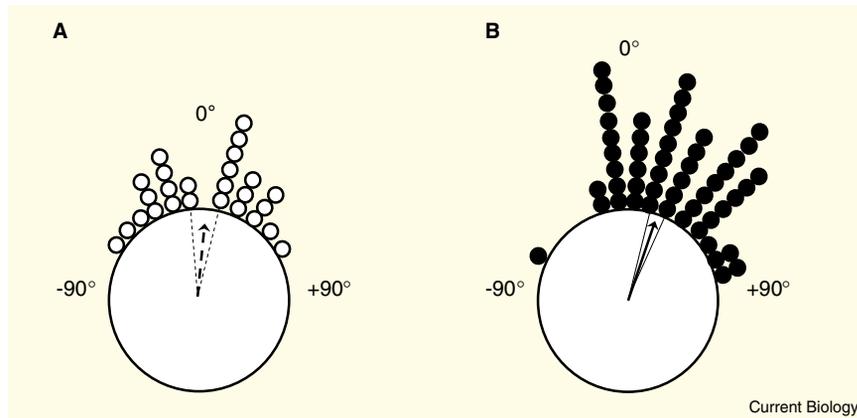


Figure 2. Mean correction angles of migrating *Autographa gamma* during spring migrations.

A correction angle (circles at periphery) of 0° indicates that the mean heading of the moths was identical to the mean displacement direction during that particular migration event. Positive values (clockwise from 0°) indicate that the moths compensated for wind-drift by heading in a direction closer towards the presumed inherited migration direction (PID = 18°) than their current displacement direction. Conversely, negative values (anti-clockwise from 0°) indicated orientation away from the PID. (A) Events where the mean displacement direction of the moths differed <20° from the PID (open circles). Dashed arrow and lines: sample mean vector (correction angle = +3°, $n = 26$) and its 95% confidence intervals ($\pm 11^\circ$). (B) Events where the mean displacement direction of the moths differed >20° from the PID (closed circles). Solid arrow and lines: sample mean vector (correction angle = +20°, $n = 25$) and its 95% confidence intervals ($\pm 6^\circ$). The figure shows that *A. gamma* moths significantly compensate for wind drift when their displacement directions are >20° from their preferred migratory direction, but not when they are <20°.

flight headings were tightly centred about a single common direction [2]. Almost all of these events (99%) had mean flight headings that were northwards (Figure 1C). The mean heading of all individual *A. gamma* (subsequently termed 'presumed inherited direction', PID) was approximately NNE (Rayleigh test, mean heading = 18°, $R = 0.17$, $P < 0.001$, $n = 23,338$) – that is, approximately 180° different from the overall PID of the autumn-generation migrants (Figure 1F) which was approximately SSW (205°) [2]. Spring-generation *A. gamma* migrants compensated for cross-wind drift in a similar manner to autumn migrants [2] by biasing their windborne tracks towards their PID.

During events when the moths' tracks drifted by only a small amount from the PID (<20°), the mean correction angle (the difference between heading and track) was small (+3°, Figure 2A) and not significantly different from zero (95% CI = 11°, $S = 0.6$, $P = 0.552$, $n = 26$). However, when cross-wind drift produced tracks that veered to a larger degree from the PID (>20°), the mean correction angle was significantly different from zero (correction angle = +20°, 95% CI = 6°,

$S = 5.9$, $P < 0.001$, $n = 52$; Figure 2B). Thus during both autumn [2] and spring migrations, when wind directions deviated from their PID, migrant *A. gamma* orient their flight headings so as to partially compensate for this drift.

Taken together, results from this study and from our earlier work [2] demonstrate that *A. gamma* uses a compass sense to guide both its forward and return migrations, with seasonal reversal of its compass-mediated flight heading. This phenomenon has previously been shown in some day-active low-flying butterflies [5,6], but the present study provides the first strong evidence of this in a high-flying nocturnal insect migrant. Our findings also show that *A. gamma* can compensate for cross-wind drift while migrating hundreds of metres above the ground at night; while this phenomenon is well-known in low-flying day-active insects [7,8], *A. gamma* is so far the only insect species known to be able to do this while flying at high-altitudes at night. The navigational compass mechanism that enables this species to migrate so successfully is not understood, but a magnetic compass is likely [2]. How this

species achieves a seasonal reversal of its flight heading is as yet unknown [3,9], but seasonal changes in day length are probably involved. Finally, we note that the present results, together with our previous paper [2], contradict, at least for *A. gamma*, the suggestion [10] that the migration of economically-important pest Lepidoptera to high latitudes is a non-adaptive consequence of recent human agricultural practices.

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