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The significance of midsummer movements of *Autographa gamma*: Implications for a mechanistic understanding of orientation behavior in a migrant moth

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Abstract The silver Y moth *Autographa gamma* undertakes windborne spring and fall migrations between winter breeding regions around the Mediterranean and summer breeding regions in northern Europe. Flight behaviors facilitating these migrations include: (i) selection of seasonally-favorable tailwinds; (ii) flying at the altitude of the fastest winds; (iii) adopting flight headings that partially counteract crosswind drift; and (iv) seasonal reversal of preferred directions between spring and fall. In the UK, radar measurements indicate that migratory activity is pronounced during the spring and fall, but is usually very low during midsummer (July). However, an atypically intense period of high-altitude flight was recorded during July 2006, and in this study we compare the flight behavior of *A. gamma* during these midsummer movements with the more typical spring and fall migrations. During July 2006, activity was most intense at significantly lower altitudes than occurred in spring or fall, and was not associated with the height of the fastest winds; consequently displacement speeds were significantly slower. The most striking difference was an absence of tailwind selectivity in July with windborne movements occurring on almost every night of the month and on tailwinds from all directions. Finally, orientation behavior was quantitatively different during July, with significantly greater dispersion of flight headings and displacements than observed in spring and fall. We discuss mechanisms which could have caused these differences, and conclude that a lack of appropriate photoperiod cues during development of the summer generation resulted in randomly-oriented ‘dispersive’ movements that were strikingly different from typical seasonal migrations [Current Zoology 59 (3): 360–370, 2013].

Keywords Long-range migration, Dispersal, High-altitude flight, Photoperiod, Entomological radar, Noctuid moths

Migration has arisen in all the major insect taxonomic lineages, and plays a central role in the population dynamics and ecology of numerous species (Johnson, 1969; Dingle, 1996; Roff and Fairbairn, 2007; Chapman and Drake, 2010; Drake and Reynolds, 2012). In the Northern Hemisphere, many billions of individuals, of a wide range of species, migrate northwards each spring from low-latitude winter breeding regions into higher latitudes of the temperate zone, to exploit seasonally-favorable habitats where they can reproduce during the summer but would be unable to survive the winter (Holland et al., 2006; Chapman et al., 2011a, 2012). Some comparatively large and fast-flying species (notably some butterflies, dragonflies and day-flying moths) often migrate close to the ground, within their flight boundary layer (FBL) where their airspeed exceeds the wind speed, thus enabling a

high degree of control over their speed and direction of movement (e.g. Srygley and Dudley, 2008). However, the vast majority of migratory insect species (including butterflies on some occasions: Mikkola, 2003; Stefanescu et al., 2012) carry out these journeys by ascending to high altitudes (typically > 100 m above the ground), where fast-moving airstreams enable considerable distances (sometimes several hundred kilometers) to be traversed in a single flight bout (Drake and Farrow, 1988; Gatehouse, 1997; Chapman et al., 2011a). In comparison to flight within the FBL, windborne migration would appear to be a rather risky and unpredictable strategy, as the distance and direction of movement will be controlled by the speed and direction of the airstreams within which the insects fly. This has led to the widely-held notion that even large windborne insect migrants, once they have

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taken off, are ‘at the mercy of the wind’ – a notion that was supported, until recently, by the comparative scarcity of observations of consistent southward return movements of migrants to regions suitable for overwintering.

The paucity of observations of these return movements was largely a consequence of the difficulty of observing insects engaged in flight hundreds of meters above the ground. However, the availability of remote sensing technologies such as entomological radars (Chapman et al., 2011a; Drake and Reynolds, 2012) and (to a lesser extent) radio-tracking (Wikelski et al., 2006), combined with advances in trajectory simulation models (e.g. Otuka et al., 2005), have enabled the documentation of the migratory routes of windborne insects in much greater detail than hitherto. These advances have revealed that large-scale return migrations to southern winter breeding grounds do indeed occur in a range of windborne migrants from several insect orders. Among the best studied insects from this perspective are nocturnally-active noctuid moth pests, and mass southward fall migrations have now been documented in, for example: *Agrotis ipsilon* and *Helicoverpa zea* in North America (Showers, 1997; Westbrook, 2008); *Helicoverpa armigera*, *Mythimna separata* and *Spodoptera exigua* in East Asia (Feng et al., 2003, 2005, 2008, 2009); and *Autographa gamma* and *Noctua pronuba* in Europe (Chapman et al., 2008a, 2008b, 2010; Alerstam et al., 2011). Southward windborne migrations in the fall have also been documented in other groups, including: dragonflies (Russell et al., 1998; Feng et al., 2006; Wikelski et al., 2006), leafhoppers (Taylor and Reling, 1986), pyralid moths (Riley et al., 1995) and butterflies (Mikkola, 2003; Stefanescu et al., 2012). It is thus becoming clear that many species of seasonal insect migrants use favorable tailwinds to carry out successful two-way journeys.

In some species, particularly the smaller and weaker-flying ones, such two-way migrations may rely on seasonal changes in prevailing wind directions to effect displacement in seasonally beneficial directions (Pedgley et al., 1995). Certain northern temperate species are known to increase their chances of migrating in a beneficial direction during the fall by preferentially migrating on days or nights when winds blow from the north, perhaps using changes in barometric pressure (Shields and Testa, 1999) or declining air temperature (Wikelski et al., 2006) as cues to indicate periods with northerly winds suitable for initiating migratory flight. Yet other species, particularly among the Lepidoptera,

appear to have evolved a range of flight behaviors that enable them to efficiently exploit high-altitude winds to achieve rapid and long-distance transport in beneficial directions. One of the best-studied species is the silver Y *Autographa gamma*, an Old World noctuid moth that carries out seasonal to-and-fro migrations between winter breeding regions around the Mediterranean Basin and summer breeding regions in northern Europe. Radar studies have shown that spring and fall migrants restrict migratory activity to nights with beneficial tailwinds (from the south during spring and from the north during fall), and after takeoff rapidly ascend to altitudes typically between 300–800 m above the ground and tend to concentrate where wind speeds are fastest (Chapman et al., 2008a, 2008b). In addition, the migrants adopt flight headings fairly close to the downwind direction in such a manner that they add a large component of their air-speed to the wind speed while also partially correcting for crosswind drift (Chapman et al., 2008a, 2008b). These flight behaviors result in migration directions that are seasonally appropriate, and nightly migration trajectories that are on average 50% longer, and 20° closer to the seasonally preferred direction (Chapman et al., 2010), than would be achieved by merely drifting downwind (Chapman et al., 2011b). Population monitoring in the UK demonstrated that high-latitude seasonal breeding results in a fourfold increase in the fall generation compared to the original spring immigrants, and simulation modeling indicated that ~80% of these fall migrants will reach the Mediterranean Basin after only 3 nights of migration on suitable tailwinds (Chapman et al., 2012).

The expression of migratory behavior and seasonal reversal of preferred directions observed in *A. gamma* (Chapman et al., 2008a) is presumably orchestrated at least in part by photoperiod and other environmental cues experienced during development (see Discussion). If this is the case, then the environment in which the larvae and pupae develop, and the adult emerges, will be critical to the population-level migratory phenotype expressed by the adults, e.g. whether they exhibit the same preferred migratory direction as their parents, have switched to the opposite direction, or show some intermediate pattern of flight behavior. The phenological pattern of migratory activity of *A. gamma* in the UK typically shows a peak of migration intensity in May and June corresponding to immigration from the south; an almost total absence of high-altitude flight activity in July (midsummer); and finally another peak of migration activity in August and September when the off-

spring of the initial immigrants migrate southwards (Chapman et al., 2012), a pattern that is similar to that observed in the mid-1930s in the UK (Fisher, 1938). However, an unusually intense period of high-altitude flight activity by *A. gamma* detected by radar during July 2006 provided an interesting natural experiment in which to investigate the effect of different developmental conditions on the flight behavior of this species during the spring, summer and fall.

1 Materials and Methods

1.1 Entomological radar operating procedures

We investigated seasonal variation in migration intensity and associated flight behaviors of high-flying *A. gamma* moths above the southern United Kingdom using data collected by two purpose-built, vertical-looking entomological radars (VLRs) situated in southwest and southeast UK. The former was at Malvern, Worcestershire (lat. 52°06'04"N, 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 onwards, while the latter radar has been at Rothamsted, Harpenden, Hertfordshire (lat. 51°48'32"N, long. 0°21'27"W) from 1999 onwards. The VLR equipment and operating procedures are described in detail elsewhere (Chapman et al., 2002, 2011a; Reynolds et al., 2005), but we provide a brief summary here. The VLRs provide a range of information – including body mass, flight altitude (insects are detected in 15 altitude bands, each of which is 45 m deep), aerial density, displacement speed, displacement direction, and flight heading – for all individually-resolvable insects with a body mass of a few mg that fly through the vertically-pointing beam, although only those >15 mg are detectable over the whole sampling altitude range of ~150–1200 m above the radar sites. The VLRs are operated for a 5-minute sampling period every 15 minutes throughout the daily cycle, thus giving a total of 16 sample periods within the 4-hour period of nocturnal flight activity (20:00–00:00 GMT) that we used in this study. Data for this study were collected from the ‘spring’ (May and June) and ‘fall’ (August and September) migration periods from three recent years of mass *A. gamma* invasions in the UK, namely 2000, 2003 and 2006 (Chapman et al., 2012, see Fig. 1), and also from the unusual peak of *A. gamma* flight activity recorded in midsummer (July) of 2006. Nightly counts of high-flying radar-detected *A. gamma* moths at each radar site were converted to aerial densities and migration fluxes as described elsewhere (Chapman et al., 2012).

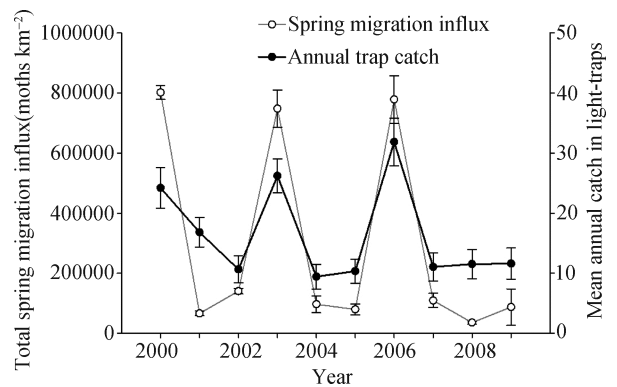


Fig. 1 Radar measurements of the total high-altitude migration intensity of *Autographa gamma* during spring of each study year plotted against the mean annual catch of this species in a national network of light traps

1.2 Identification of radar-detected *A. gamma* migration events

Aerial netting at 200 m above the ground (Chapman et al., 2004, 2010) and captures in 12 m high suction traps (Wood et al., 2009) demonstrate that the only large (>100 mg) insects that are abundant, high-altitude, nocturnal migrants in the UK are comprised of a relatively few species of noctuid moths. We can thus be highly confident that the vast majority of VLR-detected large (>100 mg) nocturnal insect targets were noctuid moths, and the aerial composition of this family in the UK is dominated by *A. gamma* in the years selected (Chapman et al., 2004, 2010; Wood et al., 2009). Only one other species of noctuid moth has been caught migrating at high altitude (200 m) above the UK – the large yellow underwing *Noctua pronuba* (Chapman et al., 2004) – but this species has a mean body mass more than twice that of *A. gamma* (Wood et al., 2009), and so radar returns produced by *N. pronuba* can be easily distinguished from those returned by overflying *A. gamma* during the initial data processing. We identified radar-detected individuals of *A. gamma* by a previously published procedure (Chapman et al., 2008b, 2010, 2012), whereby the VLR database of nocturnal insects (flying between 20:00 and 00:00 GMT) was filtered for radar targets that had an estimated body mass falling within the range of 100–200 mg, closely matching that measured for freshly-caught specimens of *A. gamma* (146 mg ± 35 mg (mean ± 1 SD), $n = 11$). Only *A. gamma* radar data collected in the spring and fall migrations of recent mass invasion years (2000, 2003 and 2006), and the midsummer movements of July 2006, were analyzed for this study. Confirmation that *A. gamma* seasonal and annual abundance at ground level closely matched radar-detected flight activity at high

altitude was provided by comparing VLR data on flight intensity with mean catches from the Rothamsted Insect Survey national network of light traps. This network contains ~100 identical light traps distributed across the whole of the UK, from which all macro-moths are identified and counted on a nightly basis throughout the year (Harrington and Woiwod, 2007). We selected 23 traps that ran continuously from 2000 to 2009, caught reasonable numbers of *A. gamma* in each year (16.4 ± 0.9 (mean ± 1 SE) per year), and provided broad geographical coverage of the UK, although they were concentrated mostly in the south (mean latitude = 52.3665°N ; see Chapman et al., 2012). Mean annual and weekly catches from these 23 traps were used as proxies for annual and weekly abundance of the total UK ground populations, and were compared directly with the radar-estimated measures of migration rates.

1.3 Statistical analysis

Radar-estimated migration rates, and mean light trap catches, of *A. gamma* were log-transformed before analysis, and then annual and weekly totals recorded by the two methods were compared with linear regression (Fig. 1 and Fig. 2). Seasonal variation in flight altitude during 2006 was investigated by analyzing the height at which the vertical profile of *A. gamma* density peaked on each night using ANOVA with flight season (spring, summer or fall) as the factor; in addition these height values for each of the three flight seasons were compared with each other by means of *t*-tests (Fig. 3). The same process was used to investigate seasonal variation in mean nightly displacement speeds of radar-detected *A. gamma* migrants (Fig. 3). In addition, the altitude of the *A. gamma* density maximum on each night was compared with the altitude of the wind-speed maximum and temperature maximum (obtained from the Met Office’s numerical weather prediction model, the ‘Unified Model’;

Wood et al., 2006) using paired *t*-tests for each flight season in 2006, to see if flight altitude was associated with vertical profiles of wind speed or temperature in any of the seasons. All altitudes and displacement speeds were log-transformed prior to analysis. Mean monthly temperatures were obtained from the Hadley Centre Central England Temperature dataset freely available online (<http://www.metoffice.gov.uk/hadobs/hadcet/>).

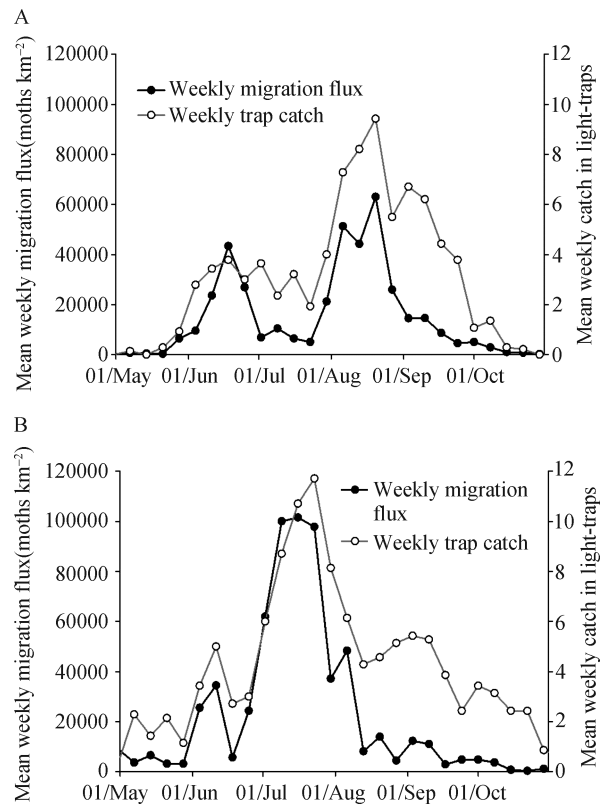


Fig. 2 Radar measurements of weekly high-altitude migration intensities of *Autographa gamma* throughout the flight season plotted against mean weekly catches of this species in a national network of light traps

A. 2000 and 2003. B. 2006.

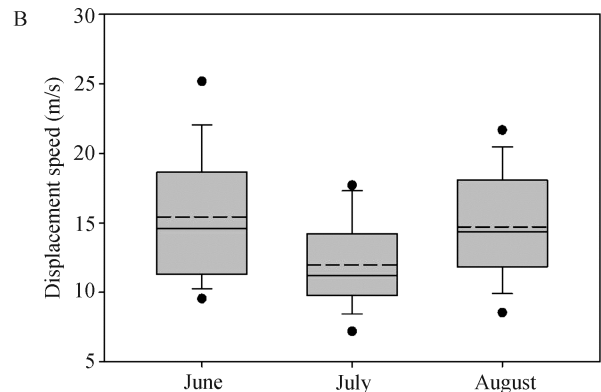
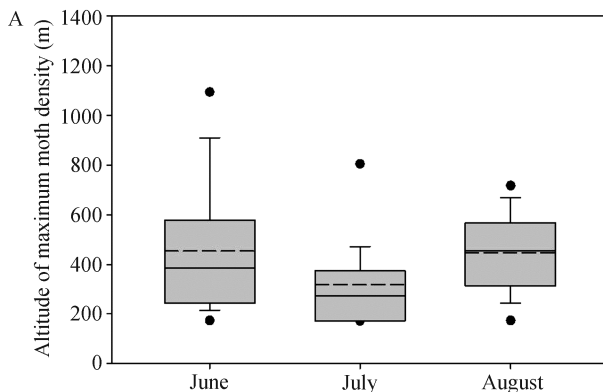


Fig. 3 Flight parameters of *Autographa gamma* during migration events in spring, summer and fall

A. Altitude of maximum moth density. B. Displacement speed. The bottom and top of the box show the lower and upper quartile values, respectively. The horizontal solid black line represents the median for each category, and the dashed line represents the mean. Whiskers indicate the 10th and 90th percentiles, while the black circles show the outliers.

1.4 Circular statistics and directional comparisons

For each individual insect that passes through the beam the VLR automatically records the displacement direction (the direction in which the insect is carried by the wind), and the body alignment (from which its flight heading – the direction in which it would fly in the absence of wind – can be calculated). Using the Rayleigh test of uniformity for circular data (Fisher, 1993), the mean displacement direction (i.e. the migration direction) and the mean flight heading, plus associated circular statistics, were calculated for all mass migration ‘events’ during the three flight seasons in 2006. We define ‘migration events’ (Alerstam et al., 2011; Chapman et al., 2012) as all the night/site counts that together comprise 90% of the cumulative total of all the individual radar-detected *A. gamma* moths in each of the flight seasons (spring, summer and fall) across both radar sites. For each migration event, the Rayleigh test was used to calculate the following three parameters for the distributions of individual displacement directions and flight headings: (i) the mean direction; (ii) the mean 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) for each distribution; and (iii) the probability that the distributions of headings and displacements differed from a uniform distribution (a P -value of < 0.05 indicates that the distribution is significantly unimodal, and hence the individual *A. gamma* in that ‘migration event’ show a significant degree of common alignment of their displacements or headings). All migration events had significantly unimodal distributions of displacement directions, reflecting the fact that they are strongly influenced by the wind which, during fair weather, is typically not expected to change its direction by any great degree during the nightly sample period (20:00–00:00 GMT). We then calculated the overall mean displacement direction of all the *A. gamma* mass migration events in 2006 for each of the following periods: 1–31 May, 1–30 June, 1–15 July, 16–31 July, 1–31 August and 1–30 September, by analyzing the individual mean displacement directions from all migration events with the Rayleigh test once again (Fig. 4). If the distribution of mean displacement directions was also significantly unimodal, we assumed that there was a significant 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.

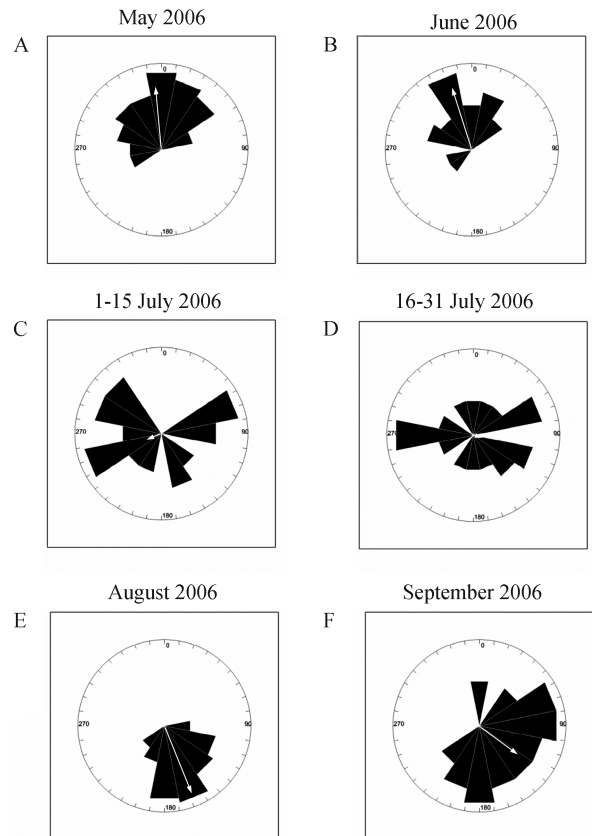


Fig. 4 Circular histograms of displacement directions during migration events throughout the flight season

The area of the black segments is proportional to the number of occasions when displacement directions fell within each 22.5° bin. The bearing of the white arrow indicates the mean direction of the entire dataset, while its length is proportional to the clustering of the dataset around the mean direction.

We then compared the following log-transformed circular variables between the three flight seasons by analysis with ANOVA (with season as the factor) and t -tests for pairwise comparisons: (i) the heading r -values from each event (a measure of the clustering of the flight headings on any one night); (ii) the displacement direction r -values from each event; and (iii) the difference between the mean heading and mean displacement direction for each event (the ‘heading offset’, an indication of how closely aligned to the downwind direction the moths’ flight headings were). For these last comparisons, to increase the sample size, heading r -values, displacement r -values and heading offsets for the spring and fall migration seasons were obtained from all migration events in the recent mass invasion years (2000, 2003 and 2006), although data from midsummer events were restricted to July 2006 (Fig. 5).

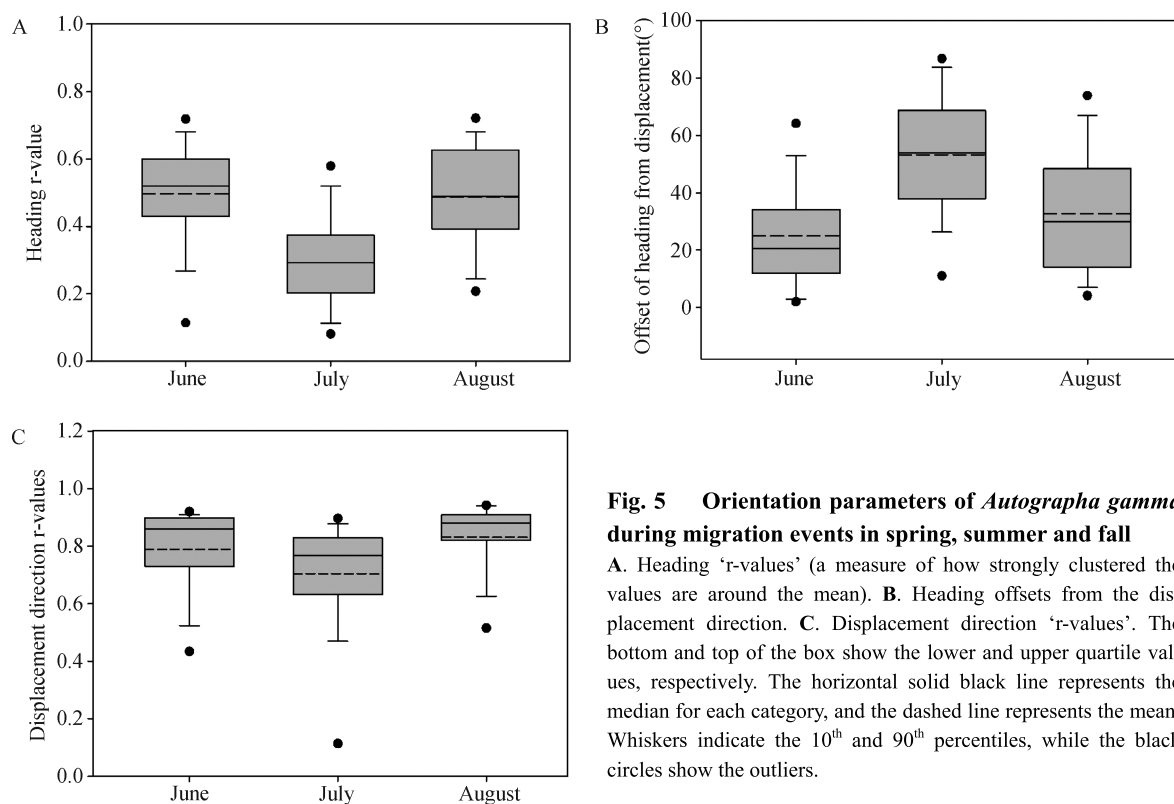


Fig. 5 Orientation parameters of *Autographa gamma* during migration events in spring, summer and fall

A. Heading ‘r-values’ (a measure of how strongly clustered the values are around the mean). **B.** Heading offsets from the displacement direction. **C.** Displacement direction ‘r-values’. The bottom and top of the box show the lower and upper quartile values, respectively. The horizontal solid black line represents the median for each category, and the dashed line represents the mean. Whiskers indicate the 10th and 90th percentiles, while the black circles show the outliers.

2 Results

The total spring influx of *A. gamma* moths into the UK in each year from 2000 to 2009 (as estimated by radar) was closely correlated with the total annual catch of *A. gamma* averaged across the national network of light traps in the same period (linear regression: $F_{1,8} = 20.5$, $r^2 = 68.5\%$, $P = 0.002$); the mass invasion years of 2000, 2003 and 2006 are clearly visible (Fig. 1). During the 2000 and 2003 invasions, there was a consistent pattern of high-altitude *A. gamma* flight activity, with strong peaks of migration intensity in the spring period (late-May through to the end of June) and the fall period (early-August through to mid-September), but very little high-altitude flight activity in July (Fig. 2A) which, as noted above, is similar to the flight pattern observed (visually) in the mid-1930s (Fisher, 1938). The radar data from 2000 and 2003 matches the seasonal pattern of weekly catches of *A. gamma* in light traps during the same period fairly well ($F_{1,50} = 113.9$, $r^2 = 68.9\%$, $P < 0.001$), although reasonably high ground-level abundance late in the season (mid-September into October) is not matched by comparable high-altitude flight activity (Fig. 2A), perhaps due to cooler air temperatures this late in the season. By contrast, the seasonal patterns of high-altitude flight activity and ground-level populations in 2006 (Fig. 2B) were strikingly different from

those in 2000 and 2003. A small immigration and associated ground-level population in May was followed by larger peaks of flight activity and ground populations in mid-June. There was then an unusual and very intense peak of high-altitude flight activity of radar targets that matched *A. gamma* during July (when migration activity in this species is not usually recorded), and the identity of these radar targets was confirmed by the extremely abundant ground-level population of *A. gamma* at this time (Fig. 2B). Finally, a rather smaller peak of migration activity occurred in the fall (early to mid-August) of 2006, but ground populations remained high until late-October. The weekly light trap catches and migration rates were strongly correlated throughout the year ($F_{1,50} = 221.6$, $r^2 = 81.2\%$, $P < 0.001$), providing evidence that the selected radar targets (including those in midsummer) were highly likely to be *A. gamma*.

We then examined the flight behavior of radar-detected *A. gamma* during July 2006, and compared our findings with the flight behaviors observed in the more typical spring and fall migrations. There was a highly significant effect of season on the mean altitude of peak flight activity (ANOVA: $F_{2,136} = 8.78$, $P < 0.001$; Fig. 3A). The mean flight altitude in July (318 ± 26 m (mean \pm 1 SE), $n = 44$ migration events) was significantly lower than the corresponding values in spring (453 ± 40 m, $n = 45$; t -test: $t = 3.04$, $df = 87$, $P = 0.003$) and fall ($447 \pm$

23 m, $n = 50$; $t = 4.34$, $df = 92$, $P < 0.001$). However, the mean flight altitudes in the spring and fall were not significantly different from each other ($t = 0.61$, $df = 81$, $P = 0.542$). During the spring migration period, the altitude of peak flight activity in each migration event was not significantly different from the altitude of the wind speed maximum at the same time (paired t -test: mean difference = 25 ± 65 m, $t = 1.37$, $df = 39$, $P = 0.177$) but was significantly higher than the altitude of the warmest air (mean difference = 289 ± 43 m, $t = 9.29$, $df = 39$, $P < 0.001$); this indicated that during spring *A. gamma* flew in the fastest airstreams rather than the warmest ones. Exactly the same pattern was observed during the fall migrations, with flight height not significantly different from the altitude of the wind speed maximum (mean difference = 33 ± 38 m, $t = 0.34$, $df = 45$, $P = 0.734$) but significantly higher than the altitude of the warmest air (mean difference = 243 ± 28 m, $t = 11.61$, $df = 45$, $P < 0.001$). By contrast, the July movements occurred at altitudes which were significantly different from both the height of the fastest winds (mean difference = 135 ± 55 m, $t = 2.21$, $df = 39$, $P = 0.033$) and the warmest temperatures (mean difference = 120 ± 26 m, $t = 5.91$, $df = 39$, $P < 0.001$), and thus there was no evidence that *A. gamma* moths emerging in midsummer selected flight heights as the spring and fall generations do.

This differential selectivity of flight height and airstreams resulted in a significant effect of flight season on displacement speed (ANOVA: $F_{2, 136} = 9.67$, $P < 0.001$; Fig. 3B). Moths travelled significantly slower in July (11.98 ± 0.45 m s⁻¹, $n = 44$) than in the spring (15.43 ± 0.70 m s⁻¹, $n = 45$; t -test: $t = 4.03$, $df = 87$, $P < 0.001$) and fall (14.71 ± 0.55 m s⁻¹, $n = 50$; $t = 3.73$, $df = 92$, $P < 0.001$). However, the mean displacement speeds in the spring and fall were not significantly different from each other ($t = 0.64$, $df = 93$, $P = 0.525$). These differences in mean displacement speed would result in moths being displaced on average about 10 km less per 1 hour flight (43.1 km per hour) in July 2006 than in the spring or fall of the same year (55.5 and 53.0 km per hour, respectively). However, there was no reduction in the flight duration of the midsummer generation, with 37% of high-flying moths detected after midnight in July, compared to 28% and 38% in June and August, respectively.

In addition to significant differences in flight altitude and movement speed, the midsummer flights were also conspicuously different in their pattern of movement directions compared to the spring and fall migrations (Fig. 4). Mean displacement directions in the spring of

2006 were consistently towards the north, in both May (Rayleigh test: mean direction = 355° , $r = 0.739$, $n = 26$ migration events, $P < 0.001$; Fig. 4A) and June (343° , $r = 0.787$, $n = 26$, $P < 0.001$; Fig. 4B), as expected. Similarly, during the fall there were consistent, and expected, southward movement directions in both August (158° , $r = 0.881$, $n = 30$, $P < 0.001$; Fig. 4E) and September (127° , $r = 0.554$, $n = 20$, $P = 0.001$; Fig. 4F), demonstrating a high degree of selectivity for seasonally-favorable tailwinds. By contrast, nightly movement directions during midsummer showed no consistent pattern, and were not significantly different from a uniform distribution in either the first half of July (no mean direction, $r = 0.155$, $n = 22$, $P = 0.597$; Fig. 4C) or the second half of July (no mean direction, $r = 0.063$, $n = 23$, $P = 0.914$; Fig. 4D), indicating a complete lack of tailwind selectivity during midsummer.

In addition to these differences in gross patterns of seasonal movement directions, there were also quantitative differences in the within-night orientation behavior of individuals during midsummer compared to the spring and fall. There was a significant effect of season on the degree of dispersion of nightly distributions of headings (ANOVA of heading 'r-values': $F_{2, 236} = 32.7$, $P < 0.001$; Fig. 5A), which was caused by the significantly lower degree of common orientation during midsummer nights than was observed in either spring (t -test: $t = 6.51$, $df = 141$, $P < 0.001$) or fall ($t = 6.78$, $df = 95$, $P < 0.001$). Furthermore, the mean offset of the nightly heading direction from the nightly displacement direction was also significantly affected by season (ANOVA of 'heading offsets': $F_{2, 215} = 19.4$, $P < 0.001$; Fig. 5B), due to considerably larger offsets occurring in July than in either spring ($t = 6.96$, $df = 126$, $P < 0.001$) or fall ($t = 5.22$, $df = 135$, $P < 0.001$). The combination of greater mean offsets and greater dispersion of individual headings during midsummer nights resulted in a seasonal effect on the tightness of displacement directions within each night (ANOVA of displacement 'r-values': $F_{2, 236} = 9.46$, $P < 0.001$; Fig. 5C), which was explained by significantly greater dispersion of displacement directions in midsummer than in spring ($t = 2.37$, $df = 79$, $P = 0.020$) or fall ($t = 3.29$, $df = 72$, $P = 0.002$).

3 Discussion

Our comparative analyses of the flight behavior of radar-detected high-flying *A. gamma* during spring, midsummer and fall of 2006 demonstrated that the midsummer movements were atypical and quantitatively different in a number of parameters from the sea-

sonal migrations characteristic of spring and fall. High-altitude movements in midsummer showed a striking lack of tailwind selectivity and consequently the overall movement patterns lacked the directional bias that is seen in the spring and fall migrations of *A. gamma* (Chapman et al., 2008a, 2008b, 2010) and other noctuid moths (e.g. Feng et al., 2008, 2009). In addition, the *A. gamma* midsummer movements occurred at significantly lower flight altitudes, and in slower airstreams, than in the spring and fall, so consequently travel speeds and movement distances were shorter. Finally, orientation behavior was significantly different between seasons too: *A. gamma* exhibited a greater range of within-night flight headings, and their headings were offset from the downwind direction by a greater degree, during the midsummer movements compared to the spring and fall. Taken together, these differences indicate that the midsummer movements were fundamentally different from the more typical seasonal migrations of *A. gamma*. Given the lack of tailwind selectivity and lack of a consistent directional bias in the nightly movement directions, the midsummer movements are perhaps better described as dispersive in nature rather than migratory, i.e. they would tend to lead to a random redistribution and mixing of the population, rather than the coherent northward and southward movements seen in the spring and fall.

Autographa gamma is incapable of overwintering in the UK (Hill and Gatehouse, 1993), and spring populations result from annual invasions from further south in the species' range (Chapman et al., 2010, 2012). These spring invasions typically occur in June, and they produce the next generation of adults which emerge in August and September, when they undertake a return migration to lower latitudes. In most years there are relatively few adult *A. gamma* on the wing in the UK during July (Fisher, 1938; Chapman et al., 2012). The provenance of the unusually large midsummer generation in 2006 therefore needs to be resolved. If the adults had immigrated from continental Europe during July, we should expect to see a preponderance of movements from either the south or east (depending on their origin), but the random pattern of movement directions throughout July (Figs. 4C, 4D) indicates that this was not the case. It is more likely that the midsummer generation of adults emerged from populations which developed within the UK, probably from eggs laid by the small influx of *A. gamma* that occurred in early-May 2006 (Fig. 2B) which, given the warmer than average conditions during summer (June 2006 was the second

warmest June since the heatwave of 1976, while July 2006 was the warmest month ever recorded in central England), could have produced the large generation of adults which emerged in July.

This generation clearly engaged in high-altitude flight on a very large scale – radar-measured nightly migration fluxes of *A. gamma* were higher in July 2006 than at any other time in the last 10 years (Fig 2). This may be because *A. gamma* is an obligate migrant, i.e. all adults of every generation embark on migration, irrespective of their developmental conditions or the quality of the habitat within which they emerge. Whatever the cause of the high-altitude midsummer flights, there appear to be three potential mechanisms that may have given rise to the marked differences we observed in the behavior of the summer dispersers in comparison to archetypal seasonal migrants. The first possible explanation is that some subpopulations (or individuals) in the UK had switched from 'spring-type' to 'fall-type' migrants during their development, while other subpopulations (or individuals) had not switched, giving rise to an unusual mixture of migratory headings and flight behaviors. This mechanism can quite quickly be ruled out however, as the directional data from July 2006 do not match this hypothesis in three key aspects. Firstly, distributions of flight headings within nights nearly always exhibited a significant degree of common orientation relatively close to the downwind direction, indicating that all individuals on any one night were attempting to fly in approximately the same direction (which was close to the downwind). Secondly, looking at nightly displacement directions across the whole month (Figs. 4C and 4D), there is no evidence of a bimodal north-south distribution of migratory directions, as you would expect if the migratory population consisted of a mixture of spring-type and fall-type migrants. Thirdly, if a mixture of spring-type and fall-type migrants were flying together, it is difficult to explain why they flew at lower flight heights, and in slower-moving airstreams, than in the spring and fall.

Another possible mechanism may be that the midsummer generation was produced by individuals from a mixture of regionally-adapted subpopulations that happened to arrive in the UK in May 2006. This was suggested by Spieth and Cordes (2012) as an explanation for some local populations of the large white butterfly *Pieris brassicae* which had flight directions which deviated by a large degree from the main north-south migration axis in Western Europe; major geographic barriers, particularly coastlines, were thought to have forced lo-

cal adaptations in regional subpopulations. Local adaptations seem much less likely in *A. gamma* because populations do not persist in Northern Europe but are replenished every year by (well-mixed) wholesale invasions from the south. Even a genetic cline in migration traits across latitude – as suggested for migratory potential in the oriental armyworm *Mythimna separata* populations in East Asia (Han and Gatehouse, 1991) – may be unlikely if *A. gamma* is forced to move from overwintering areas by unfavorably high temperature during the summer, i.e. the main populations migrate in every generation. Nonetheless, we note that populations from completely different source areas was suggested as a possible explanation of some anomalous results found in *A. gamma* from Sweden (compared to samples from Morocco, Britain and Germany) during a study of the genetic control of adult pre-reproductive period (Hill and Gatehouse, 1993) – the Swedish population might have had a source in the southwest of the former USSR, as opposed to a north-western Africa source of the British/German populations.

But in our opinion the most likely mechanism for the atypical flight behavior was the fact that the midsummer generation developed at an unusual time of year (larval development throughout June), leading to a lack of appropriate seasonal cues for adults emerging during July to switch on the developmental/physiological pathways underlying typical seasonal migratory behavior. The switch between spring-type and fall-type migrant behavior is most likely to be controlled by photoperiod duration and its direction of change (i.e. whether it is increasing or decreasing) during larval/pupal development and/or the early-adult stage, as this is the most reliable cue indicating seasonal progress. Temperature and host-plant quality may also have an effect. Migration in insects usually occurs during the relatively short pre-reproductive period (PRP) of adults, which is defined as the length of time from adult emergence until the attainment of sexual maturity (Johnson, 1969; Gatehouse, 1997). The length of the PRP (and thus the period of migratory activity), and the factors that influence it, have been extensively studied in several noctuid moth species (e.g. Han and Gatehouse, 1991; Hill and Gatehouse, 1992), but most thoroughly in *Pseudaletia (Mythimna) unipuncta*. In the latter species, the ‘sensitive period’ appears to be in the pupal and/or early-adult stage, when photoperiod and temperature conditions indicative of the onset of fall (i.e. long nights and cool temperatures) produce a significant increase in the PRP of females, thus increasing their migratory potential

(Turgeon and McNeil, 1983; Delisle and McNeil, 1986, 1987). The effect of environmental conditions upon sexual maturation (and thus migratory activity) is mediated by juvenile hormone and probably neuropeptides such as allatostatin and allatotropin (Cusson et al., 1990; McNeil and Tobe, 2001; McNeil et al., 2005). In *A. gamma*, the PRP is also extended at low temperatures and under short photoperiods, and probably extended under gradually decreasing photoperiods, although this species may respond to environmental cues throughout its larval/pupal development (Hill and Gatehouse, 1992). In moths, the main focus of investigations of the ‘migration syndrome’ has been factors controlling the duration of the PRP. However a recent study in the monarch butterfly indicated that the seasonal reversal of preferred migratory directions is modulated by exposure to a period of cold during the overwintering period (Guerra and Reppert, 2013). It seems quite likely therefore that aspects of *A. gamma*’s migration syndrome in addition to PRP duration, particularly (in the present context) the seasonally preferred heading directions and associated migratory flight behavior, are similarly influenced by photoperiod, temperature, and perhaps other cues such as host plant senescence. Development of the midsummer generation and emergence of adults around the period of the summer solstice during 2006 probably resulted in the UK population receiving conflicting environmental cues (particularly changes in photoperiod), producing adult phenotypes which expressed atypical flight behavior more akin to dispersive movements than migration.

High-altitude dispersive movements have also been observed during midsummer in the migratory pyralid moth *Loxostege sticticalis*, the beet webworm (Feng et al., 2004). This species undergoes seasonally-directed long-range spring and fall migrations like *A. gamma*, but the summer generations of *L. sticticalis* only flew for a few hours after dusk and individuals flying on the same night did not show common orientation, in contrast to spring and fall migrants which flew all night and showed common orientation in seasonally-beneficial directions (Feng et al., 2004). The summer flight behaviors were interpreted as representing short-range dispersal, and thus there is some similarity with the results of the current study. However, there are important differences too, as in our study the summer generation of *A. gamma* did not show a reduced flight duration, and individual *A. gamma* also exhibited significant common orientation (with respect to the downwind direction) within nights, although there was no consistent migra-

tory direction. Summer generations of the monarch butterfly *Danaus plexippus* also show a lack of orientated unidirectional flight when tethered experimental adults were flown in a flight simulator (Zhu et al., 2009), in stark contrast to the persistent south-westerly orientations that fall migrants take up when flown in the same experimental setup (Mouritsen and Frost, 2002; Zhu et al., 2009). However, whether free-flying natural populations of summer monarchs engage in long-range dispersive flights remains unknown. The results of the current study on *A. gamma* midsummer dispersive flight behavior are the first documented evidence of this kind of behavior in a migratory noctuid, and thus provide an important insight to the role of environmental conditions on the expression of migratory behaviors in natural populations of an insect. Further work is evidently required to identify the environmental cues which switch on the developmental pathways underlying seasonally appropriate behavior in adult *A. gamma*, but it is interesting to note that Zhu et al. (2009) found that the 'orientation' genes involved in directional flight activity and sun compass orientation in monarchs seemed to be separate from the JH-response generally involved in the reproductive status aspects of the migration syndrome.

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