Received Date : 28-Jan-2015

Revised Date : 02-Jun-2015

Accepted Date : 23-Jun-2015

Article type : Standard Paper

Editor : Jennifer Gill

Section : Behavioural Ecology

Adaptive strategies in nocturnally migrating insects and songbirds: contrasting responses to wind

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Running Head: Adaptive strategies in nocturnal migrants

Summary

1. Animals that use flight as their mode of transportation must cope with the fact that their migration and orientation performance is strongly affected by the flow of the medium they are moving in, i.e. by the winds. Different strategies can be used to mitigate the negative effects and benefit from the positive effects of a moving flow. The strategies an animal can use will be constrained by the relationship between the speed of the flow and the speed of the animal's own propulsion in relation to the surrounding air.

2. Here we analyse entomological and ornithological radar data from north-western Europe to investigate how two different nocturnal migrant taxa, the noctuid moth *Autographa gamma* and songbirds, deal with wind by analysing variation in resulting flight directions in relation to the wind-dependent angle between the animal's heading and track direction.

3. Our results, from fixed locations along the migratory journey, reveal different global strategies used by moths and songbirds during their migratory journeys. As expected, nocturnally migrating moths experienced a greater degree of wind drift than nocturnally migrating songbirds, but both groups were more affected by wind in autumn than in spring.

4. The songbirds' strategies involve elements of both drift and compensation, providing some benefits from wind in combination with destination and time control. In contrast, moths expose themselves to a significantly higher degree of drift in order to obtain strong wind assistance, surpassing the songbirds in mean ground speed, at the cost of a comparatively lower spatiotemporal migratory precision.

5. Moths and songbirds show contrasting but adaptive responses to migrating through a moving flow, which are fine-tuned to the respective flight capabilities of each group in relation to the wind currents they travel within.

Key-words: *Autographa gamma*, drift compensation, flight behaviour, noctuid moths, passerines, seasonal migration, windborne migration.

Introduction

Each spring, immense numbers of insects and birds migrate polewards into temperate regions of the world to exploit seasonal resources for reproduction, before they and/or their progeny return to lower latitudes in the autumn (Holland, Wikelski & Wilcove 2006; Hahn, Bauer & Liechti 2009; Chapman *et al*. 2010; Drake & Reynolds 2012; Stefanescu *et al*. 2013; Bauer & Hoye 2014). Long-range migration to high-latitude breeding regions confers substantial benefits to individuals which survive the journey, via several nonexclusive mechanisms. Newly arrived migrants may experience reduced rates of competition (Alerstam, Hedenstöm & Åkesson 2003), predation (McKinnon *et al*. 2010), parasitism (Stefanescu *et al*. 2012), and/or pathogen infection (Altizer, Bartel & Han 2011; Chapman, Reynolds & Wilson 2015). In addition, migrants often have increased reproductive productivity, and/or a greater number of generations per annual cycle, compared to non-migrants (Spitzer, Rejmánek & Soldán 1984; Rohwer, Hobson & Rowher 2009; Chapman *et al*. 2012; Sibly *et al*. 2012). However, these benefits will be offset by costs, as the physical act of travelling hundreds of kilometres is energetically demanding and carries an elevated risk of mortality (Sillett & Holmes 2002; Alerstam 2011; Hawkes *et al*. 2011; Drake *et al*. 2014; Klaassen *et al*. 2014). Travel costs are compounded by the fact that aerial (and aquatic) migrants move through a medium which is moving itself (Chapman *et al*. 2011b), often in a direction which will hinder progress along the '*preferred direction of movement*' (PDM; Kemp *et al*. 2012). In order to reduce the energetic cost and mortality risk associated with long-range movements, migrants are expected to have evolved mechanisms for identifying favourably-directed flows and flight altitudes / swimming depths (Dokter *et al*. 2011, 2013; Reynolds *et al*. 2010; Bishop *et al*. 2015; Fossette *et al*. 2015), and for selecting optimal headings that cope with unfavourable flows (Shamoun-Baranes & van Gasteren 2011; Hays *et al*. 2014; McLaren *et al*. 2014).

Nocturnally migrating moths often fly at altitudes between 200–800 m above the ground, where they usually aggregate in layers at the altitude of the fastest winds (Chapman *et al*. 2008a, 2008b, 2010; Alerstam *et al*. 2011). By contrast, nocturnal songbird migrants habitually fly higher, usually between 500–2500 m above the ground (Dokter *et al*. 2011, 2013), where winds are typically somewhat slower than those experienced by migrating moths. At the flight altitudes selected by migrating moths and songbirds, wind speeds are generally in the range of 6–22 m·s^{-1} (Shamoun-Baranes & van Gasteren 2011; Drake & Reynolds 2012); thus winds will either provide significant assistance, produce substantial lateral displacement (drift), or strongly oppose the movement, depending upon the direction of the flow relative to the animal's PDM and self-powered airspeed (Chapman *et al*. 2011b). Migrating songbirds have airspeeds between 8–16 m·s^{-1} (Alerstam *et al*. 2007; Karlsson *et al*. 2012; Nilsson *et al*. 2013, 2014); thus under most wind conditions, songbirds can usually make some progress along their seasonal PDM (albeit often rather slowly, and not at all in the case of strong headwinds). However, they must cope with crosswind drift whenever the downwind direction is not closely aligned with the PDM. By contrast, noctuid moths have much slower airspeeds of 3–5 m·s^{-1} (Chapman *et al*. 2010; Drake & Reynolds 2012); thus in order to progress along their seasonal PDM they must, by necessity, migrate in airstreams with a large tailwind component, and when flying in even slight crosswinds they will experience significantly more drift than songbirds.

Given these differences in flight performance in relation to wind speeds, one would expect songbirds to exert a greater degree of control over their track directions (direction of movement relative to the ground), and to have faster ground speeds, than noctuid moths. However, a comparative radar study of songbirds – Old World warblers (Sylvidae), thrushes (Turdidae) and flycatchers (Muscicapidae) – and noctuid moths (*Autographa gamma*) migrating over north-western Europe produced the surprising result that the moths, despite being much smaller and slower flying (and thus far more reliant on wind assistance), achieved the same ground speeds and track directions as the faster-flying songbirds (Alerstam *et al*., 2011). An ability to identify suitably-directed currents for providing transport along the seasonal PDM would be an advantage to all swimming and flying goal-oriented migrants, but it would be of the greatest benefit for those species with relatively limited movement capacity in relation to current speeds (noctuid moths in this case). However, the mechanisms that nocturnally-flying migrants use to determine suitable wind directions, facilitating transport along their seasonal PDM, remain to be determined. The orientation strategies (Chapman *et al*. 2011b) that these migrants employ under different wind conditions also require critical analysis.

In this study we investigate the question of orientation strategies by carrying out detailed comparative analyses of data collected in north-western Europe, comprising thousands of radar tracks of night-flying songbirds above southern Sweden (*n* = 4,178), and *A. gamma* moths above southern England (*n* = 8,184), during multiple spring and autumn migrations. In order to determine the seasonal PDM, the amount of lateral drift experienced, the orientation strategies utilized, and the degree of compensation achieved, robust statistical methods (Green & Alerstam 2002; Karlsson *et al*. 2010; Grönroos, Green & Alerstam 2013) have been employed. Our primary aim is to carry out, for the first time, identical quantitative analyses of the orientation responses of *A. gamma* moths and songbirds to wind flows, which allow us to classify their orientation strategies within a conceptual framework (see Chapman *et al*. 2011b) in a comparative manner, enabling a better understanding of the precise relationships between winds, flight behaviours and resulting migration directions in songbird and noctuid moth migrants.

Materials and methods

ORNITHOLOGICAL RADAR TRACKING AND DATA ANALYSIS

Nocturnal passerine migrants were recorded with X-band (3.2 cm wavelength) tracking radars (200 kW peak power, 0.25 μs pulse duration, 504 Hz pulse repetition frequency, 1.5° beam width) in Lund, south Sweden (spring: 13-27/4 1999, 28/4-25/5 2004, 2/5-7/6 2006, 6/5-10/6 2008; autumn: 22/9-11/10 1999, 25/7-31/8 2006, 8-26/8 2008) and Falsterbo, south Sweden (spring: 7/4-26/5 2010, 10/4-31/5 2011; autumn: 19/8-21/10 2009, 11/8-14/9 2010, 24/8-24/10 2011). Lund and Falsterbo data were highly consistent, and are therefore combined. All tracks were collected during dark hours, ~3–4 hours either side of midnight (local time). The radar operator searched for echoes from migrating birds by scanning manually at a range of antenna elevations between ~5 and 40°. After finding a target, typically at distances of between 2 and 6 km, the radar was switched into automatic tracking mode, and readings of azimuth, elevation and range were transferred to a computer every 2 s. Discrete Fourier transformation analysis was applied to the echo signature data, and only targets that were considered to be single individual songbirds (indicated by the characteristic radar echo signature pattern associated with bounding flight typical of songbirds) were included in this study. Minimum tracking time for each target was 30 s, with mean tracking time ~60 s. Wind data were measured within 2 h of all bird tracks, by releasing and tracking helium balloons with reflectors. Songbird airspeed and heading direction were calculated by subtraction of the wind vector at the altitude where the bird was flying from the bird's track and ground speed vector. Overall mean speeds (ground speed, airspeed, vertical speed and wind speed), directions (track direction, heading direction and wind direction) and flight altitudes (above the radar) were calculated for each individual songbird. A few tracks with airspeeds < 5 or > 20 m$\cdot$s^{-1} were excluded, as these are unrealistic values for migrating songbirds. To be directly comparable with moth data, means of all variables were calculated for each night of 'mass migration', which was achieved by restricting analysis to nights with 25 or more individual tracks (comprising 4,178 tracks from 89 nights, accounting for 83% of the total sample of individual tracks collected during the study period). The radar operating procedures and data handling have been described in further detail elsewhere (Bäckman & Alerstam 2003; Karlsson *et al*. 2012).

ENTOMOLOGICAL RADAR OPERATING PROCEDURES AND DATA ANALYSIS

We studied the flight behaviour of silver Y moths *Autographa gamma* engaged in spring and autumn high-altitude migratory flights using data collected by two purpose-built, X-band vertical-looking entomological radars (VLR) situated in inland southern England. The first has been at Rothamsted, Harpenden, Hertfordshire (lat. 51° 48’ 32” N, long. 0° 21’ 27” W) from 1999 to present; the second 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 to present. The VLR equipment and operating procedures are described in detail elsewhere (Chapman *et al*. 2002, 2003, 2011a). Briefly, individual targets flying within 15 defined altitude bands above the radar (between 150–1188 m) are interrogated when they pass through the vertically-pointing beam. These height-bands are 45 m deep and separated by a 26-m non-sampling interval. Usually, the majority of signals are resolved, and the analysis procedure yields the horizontal speed, displacement direction (track), body alignment, and three radar scattering parameters of each insect (from which body mass and shape factors are calculated). Migrating *A. gamma* moths were identified by restricting the analysis to the spring (May and June) and autumn (August and September) migration periods of 3 recent mass invasion years of this species (2000, 2003 and 2006), and then using the well-established methodology of separating radar targets produced by this species from other insects based on characteristics of the returned signals and timing of flight activity (Chapman *et al*. 2008a, 2008b, 2010, 2012). Means of all variables were calculated for each night of ‘mass migration’, which was achieved by restricting analysis to nights with 25 or more individual tracks recorded during a 2-hour period from 22:00 – 00:00 GMT and within a height range of 300–600 m above the ground (comprising 8,184 tracks from 118 nights, accounting for 78% of the total sample of *A. gamma* moths detected during the selected 2-h time period and 300-m altitude range of the study period).

STATISTICAL ANALYSIS

Using the Rayleigh test of uniformity for circular data (Fisher 1993), the mean track (i.e. the migration direction relative to the ground) and the mean flight heading, plus associated circular statistics, were calculated for all mass migration nights of songbirds and *A. gamma*. For each mass migration night, the Rayleigh test was used to calculate the following three parameters for the distributions of individual tracks and flight headings: (i) the mean direction; (ii) the mean vector length ‘*r*’ (a measure of the clustering of the angular distribution of headings or tracks 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 tracks and headings differed from a uniform distribution (a *P*-value of < 0.05 indicates that the distribution is significantly unimodal, and hence the individuals in that mass migration event show a significant degree of common alignment of their tracks or headings). All mass migration nights had significantly unimodal distributions of tracks and headings. We then calculated the overall mean track and heading directions of the songbird and *A. gamma* mass migration events in the spring and autumn periods, by analysing the nightly mean tracks and headings with the Rayleigh test once again (Fig. 1). The seasonal distributions of track and heading directions for songbirds and moths were also significantly unimodal, and we therefore assumed that both taxa had a consistent preferred direction of movement (PDM) during each migration season. These preferred directions, and the orientation strategies employed to achieve movement along the PDM, were identified by the regression method of Green & Alerstam (2002) as described in the results section.

Results

DIRECTIONS AND SPEEDS

Mean track directions (movement relative to the ground) of both taxa were northwards in the spring (songbirds: mean direction = 23°, *n* = 47 nights; moths: 348°, *n* = 43 nights; Fig. 1) and southwards in the autumn (songbirds: 183°, *n* = 42 nights; moths: 187°, *n* = 75 nights; Fig. 1), similar to previous reports (Chapman *et al*. 2010; Karlsson *et al*. 2010). Songbirds and moths also had overall mean headings in seasonally-adaptive directions, relatively close to the corresponding track directions, during both spring (songbirds: 13°, *n* = 47 nights; moths: 354°, *n* = 43 nights; Fig. 1) and autumn (songbirds: 217°, *n* = 42 nights; moths: 204°, *n* = 75 nights; Fig. 1). Even though the migration performance of songbirds and moths converged on similar movement directions, headings and speeds (see Alerstam *et al*. 2011), they employed different adaptive strategies to achieve this, as there were clear differences in the wind currents selected by songbirds and moths for migration. Songbirds migrated under a wide range of wind directions in both seasons, but most frequently on downwind directions towards the east (spring: 89°, *n* = 47 nights; autumn: 99°, *n* = 42 nights; Fig. 1), which is the prevailing wind situation in this area of Sweden. By contrast, moths selected a narrower range of wind directions, and mass migration events were restricted to nights when downwind directions were seasonally-favourable, i.e. towards the north in the spring (345°, *n* = 43 nights; Fig 1) and towards the south in the autumn (179°, *n* = 75 nights; Fig. 1).

In addition, songbirds migrated on significantly slower winds than moths (2-way analysis of variance (ANOVA), effect of taxa: $F_{1,203} = 53.7$, $P < 0.001$), and although wind speeds in general did not differ between spring and autumn (2-way ANOVA, effect of season: $F_{1,203} = 0.04$, $P = 0.838$), there was a significant interaction, indicating that winds utilised by moths during spring were the fastest of all (2-way ANOVA, taxa x season interaction: $F_{1,203} = 13.5$, *P* < 0.001; Fig. 2a, Table 1). It was not possible to directly measure the airspeed (self-powered flight speed) of the moths (which was assumed to be 4 $m \cdot s^{-1}$ in both seasons; Chapman *et al.* 2010), but songbirds had significantly faster airspeeds in spring than in autumn ($t = 2.72$, $n = 89$, $P = 0.008$; Table 1). The fast and favourably-directed winds selected by *A. gamma* moths resulted in this taxon achieving significantly greater ground speeds (movement speeds during a bout of migration) than songbirds (2-way ANOVA, effect of taxa: $F_{1,203} = 16.5$, $P < 0.001$), while the greater airspeed of songbirds in the spring and the stronger tailwinds used by moths in the spring resulted in a significant seasonal effect on ground speeds (2-way ANOVA, effect of season: $F_{1,203} = 13.8$, $P < 0.001$; Fig. 2b, Table 1). Songbirds typically migrated in airstreams which were somewhat slower than their self-powered airspeeds (ratio of wind speed to airspeed: mean 0.62 ± 0.29 SD; Fig. 2c), while moths nearly always migrated in airstreams which moved considerably faster than their airspeed (ratio of wind speed to airspeed: 2.88 ± 1.09; Fig 2c).

ORIENTATION IN RESPONSE TO WINDS

Chapman *et al.* (2011b) defined eight orientation strategies that a flying or swimming animal can exhibit with respect to the flow direction. Of those eight strategies, five are relevant to this study, as follows (in order of increasing shifting of the track away from the flow direction and towards the PDM; Fig. 3): (*i*) '*downstream orientation*' (taking up a heading coincident with the flow); (*ii*) '*compass-biased downstream orientation*' (shifting the heading a small amount from the flow direction towards the preferred direction, so that it lies between downstream and the PDM); (*iii*) '*full drift*' (maintaining a heading in the direction of the PDM irrespective of the flow direction); (*iv*) '*partial compensation*' (shifting the heading further from the flow, so that it lies on the other side of the PDM from the downwind direction); and (*v*) '*complete compensation*' (shifting the heading even further from the flow, so that the resulting track becomes coincident with the PDM). To identify the PDM and determine the orientation strategy of songbirds and moths in each season, we used the method of Green & Alerstam (2002). This method involves plotting the mean track direction on each night against the value of α (the angle between the mean track and mean heading; Fig. 3) for each night, and we did this separately for songbirds and moths during spring and autumn migrations (Fig. 4). The value of the track direction at the intercept with $\alpha = 0$ corresponds to the PDM, while the slope of the regression line indicates the orientation strategy employed: slope = 0 indicates '*complete compensation*', slope > 0 and < 1 indicates '*partial compensation*', slope = 1 indicates '*full drift*', slope > 1 indicates '*compass-biased downstream orientation*'; in the case of '*downstream orientation*' there will be no difference between track and heading ($\alpha = 0$) and thus all data points would fall on a vertical line

(Green & Alerstam 2002).

Our results indicated that spring songbird migrants had a PDM towards the NNE (18°), and the regression slope of 0.5 indicated a strategy of *partial compensation*, by which they managed to compensate for 50% on average of the wind-induced drift away from the PDM (Fig. 4, Table 2). The autumn PDM of songbirds was reversed by ~180° compared to the spring direction, lying between SSW and SW (214°; Fig. 4, Table 2). The regression slope in the autumn (0.90) indicated a strategy of a smaller degree of *partial compensation*, compensating for just 10% of wind-induced drift on average (although a strategy of *full drift* cannot be ruled out as the 95% CI just overlap with 1; Table 2). The spring and autumn regression slopes were significantly different from each other (Table 3).

Moths showed a lower degree of compensation than the songbirds in both seasons (Table 3). During spring migration, although there was some variation between years (Fig. S1a) and sites (Fig. S1b), the regression slope for the combined data corresponded to the case of *full drift* (i.e. maintaining a constant course towards the PDM irrespective of the wind), as the regression slope (0.93) was not significantly different from 1 and the 95% CI greatly exceeded 1 (Fig. 4, Table 2). The regression analysis for the combined data indicated that the PDM was very close to north (353°); thus it seems likely that the PDM of spring migrating *A. gamma* moths is northwards, and they selected flight headings and tailwinds (whenever possible) in this direction, with little attempt to correct for drift. During the autumn, the PDM of the moths was very similar to the songbirds, also lying between SSW and SW (210° for the combined data; Fig. 4, Table 2), and there was very little variation in the predicted PDMs between years (Fig. S2a) and sites (Fig. S2b), with values between 203° and 219° in all cases. However, the regression slope for the combined data was considerably larger than 1 (1.99), and the 95% CI did not overlap with 1 (Table 2), corresponding to a strategy of '*compass-biased downstream orientation*' (*CBDO*). These results were robust and only changed slightly (PDM 211°, slope 1.74) when tested with only nights with track directions between 90–270°, indicating that the circular nature of the autumn data was not a problem. When combined with selection of broadly favourable winds, the strategy of *CBDO* maximizes the speed of transport while also somewhat influencing the direction of transport when the downwind direction is not that closely aligned with the PDM (Chapman *et al*. 2011b). Testing the possible differences in orientation responses to wind for different variables (Table 3) demonstrated that moths and songbirds oriented in significantly different ways, so that track directions were more affected by wind (steeper slopes) for moths than for songbirds in both seasons. In addition, the orientation of moths and songbirds differed between seasons, with track directions being more affected by winds during autumn than spring in both taxa. There were no significant differences in the orientation responses to wind depending on wind speed or altitude, except for songbirds in autumn, which showed a pattern of more extensive drift with higher wind speed (Table 3).

Discussion

Our study is the first detailed comparative analysis of the orientation behaviour of migrating songbirds and insects, and provides new insights into the evolution of migration strategies in these groups. The results demonstrated that track directions of songbirds and moths were clearly influenced by wind (with the angle α reflecting potential wind influence), but that the drift effect was stronger for moths than for songbirds (steeper slopes in Fig. 3, Table 3). It is very likely that this drift effect to a large degree reflects the orientation of individuals under changing wind conditions, but it should be noted that the results may possibly be biased by differential departures of migrant populations with different PDMs under different wind conditions, causing so-called 'pseudo-drift' (Evans 1966; Nisbet & Drury 1967; Alerstam 1978). However, in this study we conclude that pseudo-drift is of less importance than individual orientation to account for the observed drift effects, in both the songbirds and moths, for the following reasons. In the case of *A. gamma* moths, only a single species is involved and inter-population differences in orientation behaviour over UK airspace are extremely unlikely in such a widespread insect migrant. In the case of the songbirds migrating over Sweden, recent radio telemetry studies during autumn migration in southern Sweden (Sjöberg *et al*. 2015) have verified true drift, as individually-tracked nocturnal songbird migrants (from a range of species) with preferred south-westerly orientation were regularly drifted by westerly winds to south-easterly courses. This supports the assumption that true drift is of much greater importance than pseudo-drift to explain the drift effects recorded in the current study.

Songbirds and moths were exposed to very different wind speeds relative to their own self-powered airspeeds, such that the mean relative wind speed (wind speed divided by airspeed) was 0.5–0.7 for the songbirds and 2.6–3.3 for the moths (Table 1, Fig. 2c). Hence, for songbirds the airspeed/heading vector is of primary importance in the triangle of velocities. In the ornithological literature it is most common to consider the effect of adding a smaller wind vector and to evaluate if and to what degree the heading/airspeed vector is directed into the wind to counteract drift from PDM. In contrast, for moths (and other insects) the wind vector is of dominating importance, and the discovery that migrating moths have adaptive orientations (Chapman *et al*. 2008a), rather than merely random ones, means that we are obliged to consider how the addition of a smaller heading/airspeed vector can modify the resulting track direction, considering the much larger effect of the downwind vector.

When wind speeds exceed the animal's airspeed the resulting track direction can only be modified by a limited amount from the downwind direction (Chapman *et al*. 2011b). This is the situation for the moths, which can modify the track direction up to only 18–23° away from the downwind direction at the mean wind speeds experienced in this study. Thus moths typically migrate under wind conditions that are prohibitive for achieving complete compensation and maintaining a resulting track direction towards the PDM. To achieve this, moths would have to restrict migration to nights with downwind directions very close to the PDM, or alternatively fly in much slower winds. These choices would be associated with severely negative consequences: either a reduced number of nights available for migration, or reduced travel speed, respectively. One would think that it might be useful for the moths to direct their self-vector towards the PDM, adopting the strategy of full drift (Fig. 3). This was the strategy observed during their spring migration, but during the autumn moths employed a strategy of *compass-biased downwind orientation* (*CBDO*), whereby they shifted their heading away from the downwind direction and towards the PDM by only a small degree (typically not as far as the PDM), and only when the downwind direction was > 20° from the PDM (Chapman *et al*. 2010). Although a strategy of *CBDO* provides a very high ground speed this behaviour would often render it difficult to reach a well-defined goal in an economical way (compensation flights would be required after the extensive drift). Migratory birds generally have much more narrowly defined goal areas and arrival times compared to insects, which is probably a crucial reason why they do not favour very high ground speed at the expense of extremely high drift as moths seem to do.

The orientation responses (Fig. 3) of individuals passing a fixed site under different wind conditions, as recorded in this study, *may* reflect the responses adopted throughout the migratory journey – in which case the local strategies observed in the current study (Fig. 4, Table 2) correspond to global strategies. Hence, a global strategy of (i) *complete compensation* may be adaptive when winds remain constant along the migration route (Alerstam 1979a; McLaren *et al*. 2014), while (ii) *full drift* may be adaptive if completely balanced winds from the left and right occur along the migration route (Alerstam 1990; McLaren *et al*. 2014), and also in some cases with unbalanced winds if the constant vector orientation (PDM) is flow-adjusted (McLaren *et al*. 2014). The adaptive value in (iii) a global strategy of *compass-biased downwind orientation* (also termed '*over-drift*'; Green & Alerstam 2002) lies in the exploitation of favourable tailwinds in combination with some degree of corrective orientation towards the preferred direction of movement, allowing the moths to fly with following winds from a wider sector than they would be able to do with pure downwind orientation without losing too much in destination accuracy (Chapman *et al*. 2008a). This strategy may be particularly favourable for flights through strong rotational flows (McLaren *et al.* 2014).

However, global orientation strategies may be more complex, with different responses to wind in different regions/situations along the migration route. One such global strategy in birds is that of (iv) '*adaptive drift*', where drift is adjusted to minimize the remaining distance to the destination after each flight step. If winds are shifting more or less randomly between different flight steps, it will be optimal to use a flexible behaviour of *partial compensation*, with more drift far away from the destination and more compensation near the destination (Alerstam 1979a). Another complex global strategy is that of (v) '*combined drift and overcompensation*', which is optimal under certain conditions of predictable horizontal or vertical shear flow patterns along the migration route (Alerstam 1979b; Hays *et al*. 2014; McLaren *et al*. 2014).

Since songbirds can master winds to a much higher degree than insects, strategies involving compensation are generally feasible only for songbirds (cf. McLaren *et al*. 2014). Thus, while all five global strategies are possible for birds, only the strategies of *full drift* or *CBDO* (or straightforward *downstream orientation*) seem to be feasible for moths (global strategies (ii) and (iii) above). Our results of *full drift* (autumn) or *partial drift* (spring) among the songbirds agree mainly with global strategies (ii) and (iv), while global strategies (i) and (iii) can be excluded for the songbirds. The pattern of increased drift in autumn compared to spring is in agreement with strategy (iv), since the songbirds were recorded at rather northerly latitudes when they were far away from their destinations (winter area) during autumn, but closer to their destinations (breeding area) in spring. Another possible contributory cause of the extensive drift in autumn may be the large fraction of young birds during autumn migration, since young migrants may be more likely to use vector orientation strategy (ii) (Berthold 2001; Thorup *et al*. 2003). The significant effect of wind speed on drift behaviour of songbirds in autumn may indicate that more complex responses to wind shear are involved (global strategy (v)). The strategy of combined drift and overcompensation in vertical shear flow has been observed mainly among diurnal passerine migrants (Alerstam 1979b). The results for the moths are in agreement with overall strategies (iii) in the autumn, and (ii) or (iii) in the spring, while other global strategies can be excluded.

CONCLUSIONS

Moths and passerines show contrasting adaptive responses to migrating through a moving flow. Insects are constrained by their limited self-propelled airspeeds, but take advantage of wind assistance to a much higher degree. Insects use strategies of *full drift*, *compass-biased downstream orientation* and *active downstream orientation* to maximize the amount of wind assistance, gaining fast ground speeds at the cost of precision in time and space. Waiting for the right wind conditions to occur will however increase the total duration of migration and limit the total migration distance in years with a low frequency of favourable tailwinds.. Songbirds on the other hand, with their strategy of *partial compensation* retain temporal and spatial control over their journey, but adoption of this strategy requires that they do not wait to fly only on nights with the most favourable winds but that they regularly travel on nights with crosswinds and opposing winds too.

Acknowledgements

Rothamsted Research is a national institute of bioscience strategically funded by the UK Biotechnology and Biological Sciences Research Council (BBSRC). Radar studies of bird migration were supported by grants from the Swedish Research Council. We acknowledge the support provided by COST - European Cooperation in Science and Technology through the Action ES1305 “European Network for the Radar Surveillance of Animal Movement” (ENRAM). The authors declare that they have no conflict of interest.

Data accessibility

Data are available at the Dryad Digital Repository: doi:10.5061/dryad.41sn4 (Chapman *et al*. 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1a. Linear regression of migratory track against α (the angle between track and heading) for moths during the spring in the three study years (2000, 2003 and 2006).

Fig. S1b. Linear regression of migratory track against α (the angle between track and heading) for moths during the spring at the three study sites (Chilbolton, Malvern and Rothamsted).

Fig. S2a. Linear regression of migratory track against α (the angle between track and heading) for moths during the autumn in the three study years (2000, 2003 and 2006).

Fig. S2b. Linear regression of migratory track against α (the angle between track and heading) for moths during the autumn at the three study sites (Chilbolton, Malvern and Rothamsted).

Figure Legends

Fig. 1. Distributions of track, heading and downwind directions during mass migrations of songbirds and noctuid moths (*Autographa gamma*). Small filled circles on the periphery of the large circles represent the mean direction on each night: red, inner circles are moth data and blue, outer circles are songbird data. Migratory track directions were northwards during spring (songbirds: mean direction = 23°, vector directedness (r) = 0.94, $n = 47$ nights, $P < 0.001$; moths: 348°, $r = 0.80$, $n = 43$ nights, $P < 0.001$) and southwards during autumn (songbirds: 183°, $r = 0.79$, $n = 42$ nights, $P < 0.001$; moths: 187°, $r = 0.54$, $n = 75$ nights, $P < 0.001$). Flight headings were also northwards during spring (songbirds: 13°, $r = 0.94$, $n = 47$ nights, $P < 0.001$; moths: 354°, $r = 0.84$, $n = 43$ nights, $P < 0.001$), and southwards during autumn (songbirds: 217°, $r = 0.94$, $n = 42$ nights, $P < 0.001$; moths: 204°, $r = 0.67$, $n = 75$ nights, $P < 0.001$). Downwind directions during mass migration nights were more variable: songbirds migrated on winds blowing towards a wide variety of directions, but with a significant bias towards the east (spring: 89°, $r = 0.28$, $n = 47$ nights, $P < 0.005$; autumn: 99°, $r = 0.56$, $n = 42$ nights, $P < 0.005$), while moth migrations occurred almost exclusively on seasonally-favourable tailwinds (spring: 345°, $r = 0.76$, $n = 43$ nights, $P < 0.001$; autumn: 179°, $r = 0.49$, $n = 75$ nights, $P < 0.001$).

Fig. 2. (a) Mean wind speeds associated with spring and autumn migrations of songbirds and *A. gamma* moths. Songbirds migrated on significantly slower winds, most noticeably in the spring. (b) Mean ground speeds associated with spring and autumn migrations of songbirds and *A. gamma* moths. A combination of slower tailwinds, and less selectivity of favourably-directed tailwinds, resulted in songbirds having slower ground speeds than moths in both seasons. (c) Relationship between wind speed and self-propelled airspeed for moths

(red) and songbirds (blue), shown as the ratio of wind speed over airspeed (drawn on a log scale). Dotted line indicates a ratio of 1, above which the wind speed is greater than the airspeed. Airspeed of moths is assumed to be 4 m·s^{-1}. Means and standard deviations of data in (a, b) are presented in Table 1.

Fig. 3. Triangles of velocities for five possible orientation strategies in response to flows, modified from (Chapman *et al*. 2011b). Each diagram shows the downwind vector (solid black line), heading vector (solid coloured line), track vector (dashed coloured line), and the preferred direction of migration (PDM; dashed grey line) for each strategy under the same conditions (downwind direction = 135° and PDM = 200° in all cases). The angles α (the angle between track and heading), β (the angle between downwind and track), and δ (the angle between downwind and heading) are illustrated. The regression slopes expected for each strategy when data is plotted as in Fig. 4 are shown beneath each triangle of velocities. *CBDO* = compass-biased downstream orientation, which may also be called '*over-drift*'.

Fig. 4. Analyses of the extent of drift and degree of compensatory flight behaviour in songbirds (a, b; blue circles) and moths (c, d; red circles) during the spring (a, c) and autumn (b, d). Mean track is plotted against α (the angle between track and heading) for each mass migration night, following Green & Alerstam (2002), so that orientation responses to winds from different directions can be investigated. The regression lines show the change in track direction resulting from the combined effect of the downwind direction and the flight heading, for spring migrations of songbirds and moths (left panel) and autumn migrations of songbirds and moths (right panel). Slopes and intercepts (estimates of orientation strategy and preferred direction of movement, respectively, in each taxa and season) are presented in Table 2.

Table 1. Wind speeds, ground speeds and airspeeds of migrating songbirds and moths

	Migration nights	Wind speed ± 1 SD ($m \cdot s^{-1}$)	Ground speed ± 1 SD ($m \cdot s^{-1}$)	Airspeed ± 1 SD ($m \cdot s^{-1}$)
Songbirds spring	47	6.77 ± 3.22	13.48 ± 3.32	12.70 ± 0.97
Moths spring	43	13.21 ± 4.66	16.57 ± 4.58	4.00*
Songbirds autumn	42	8.80 ± 3.89	12.14 ± 3.53	12.05 ± 1.43
Moths autumn	75	10.58 ± 3.89	13.75 ± 3.78	4.00*

*Moth airspeeds were set at 4.00 $m \cdot s^{-1}$ and were not measured in this study.

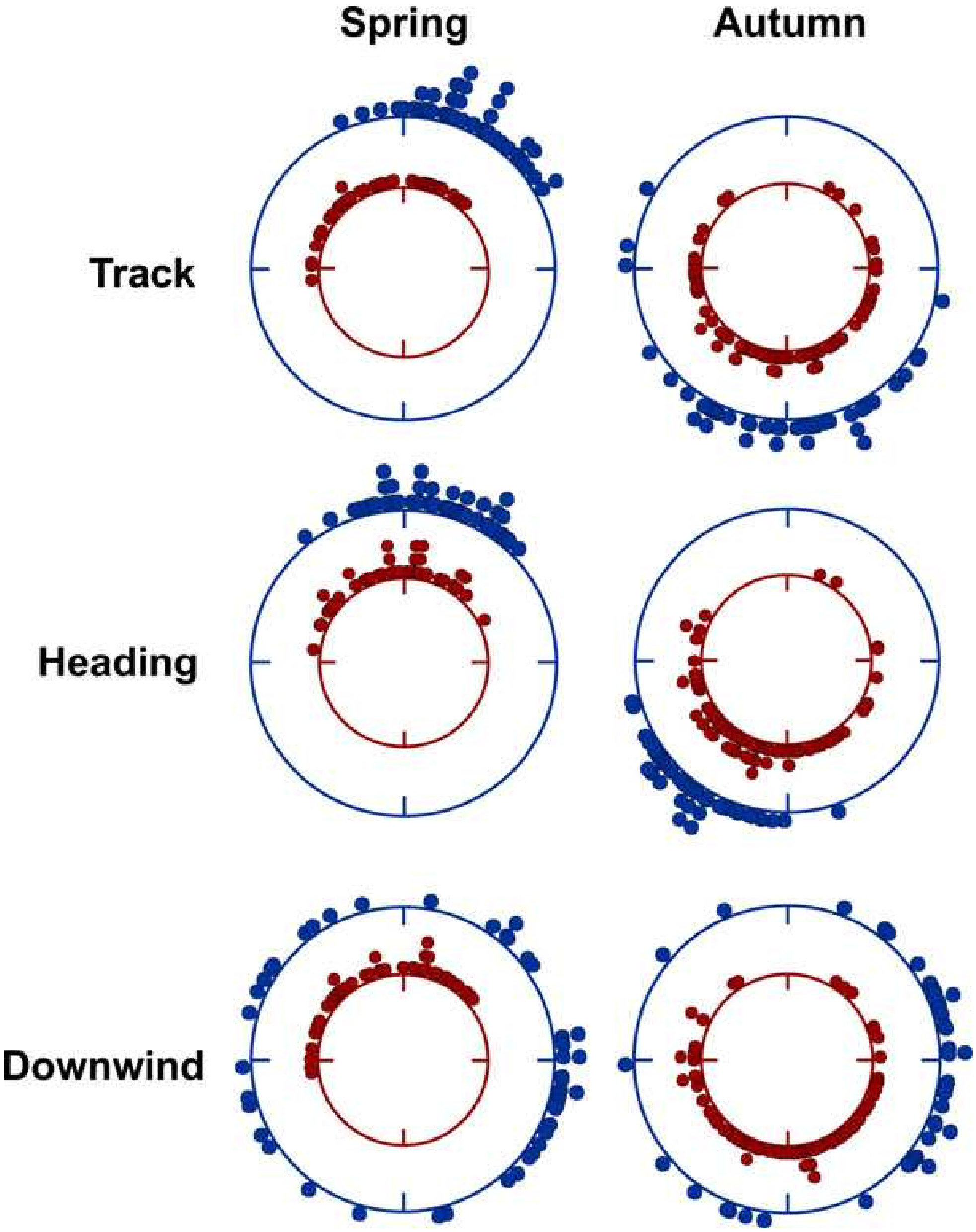
Table 2. Slopes and intercepts for the regressions of track direction in relation to the angle between track and heading direction (α)

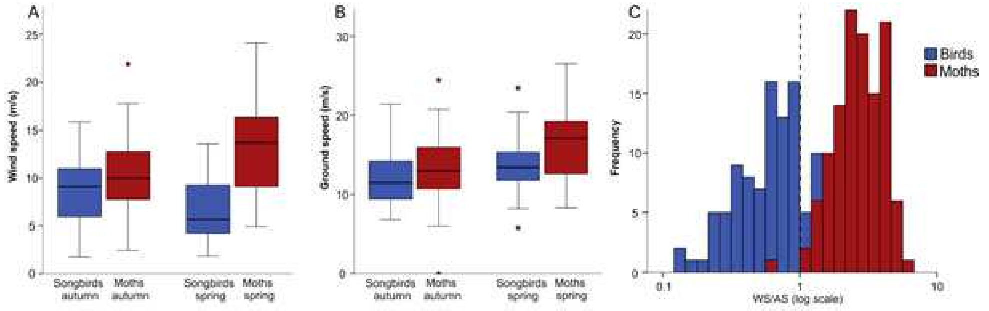
	N (nights)	Slope (95% CI)	Corresponding strategy	PDM (intercept)	*P*-value of slope	R^2
Songbirds spring	47	0.50 (0.35–0.65)	*Partial compensation*	18°	<0.001	0.45
Moths spring	43	0.93 (0.39–1.48)	*Full drift*, *CBDO*	353°	<0.001	0.21
Songbirds autumn	42	0.90 (0.74–1.05)	*Partial/full drift*	214°	0.001	0.78
Moths autumn	75	1.99 (1.35–2.61)	*CBDO*	210°	<0.001	0.35

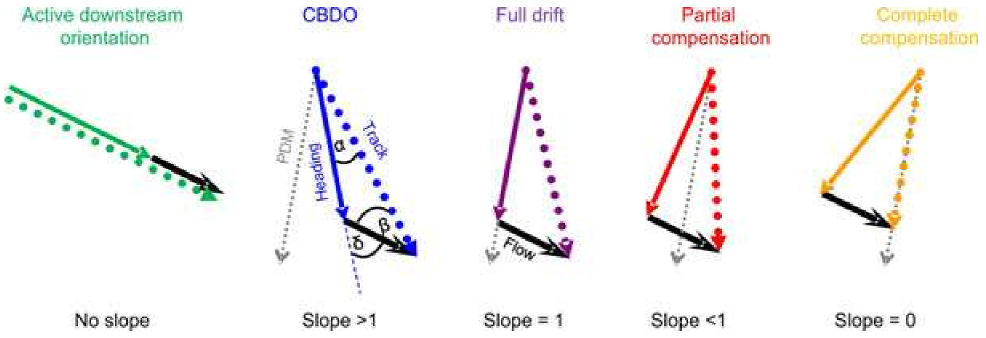
Table 3. Tests of differences in orientation responses to wind

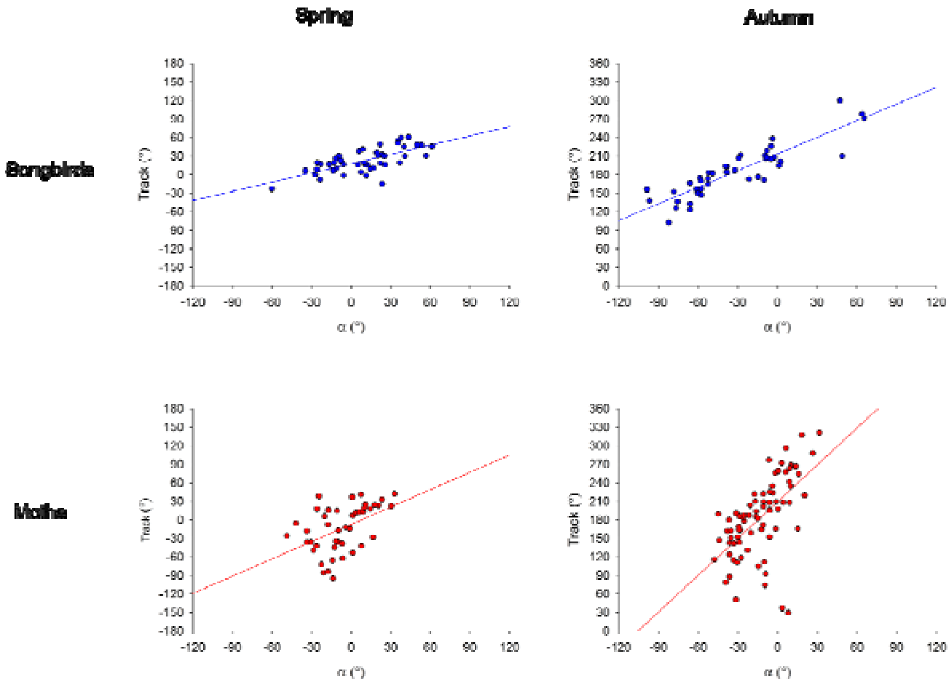
Variable	Case	Effect on drift	Test statistic	P-value
Taxon	Spring	More drift in moths than birds	$F_{1,80.7} = 9.9$	0.002
	Autumn	More drift in moths than birds	$F_{1,113} = 12.1$	0.001
Season	Moths	More drift in autumn than spring	$F_{1,112.3} = 5.3$	0.023
	Songbirds	More drift in autumn than spring	$F_{1,85} = 12.7$	0.001
Wind speed	Moths, spring	No difference	$F_{1,37.1} = 0.1$	N.S.
	Moths, autumn	No difference	$F_{1,71} = 2.6$	N.S.
	Songbirds, spring	No difference	$F_{1,41.7} = 1.9$	N.S.
	Songbirds, autumn	More drift in high wind speeds	$F_{1,37.2} = 10.6$	0.002
Altitude	Songbirds, spring	No difference	$F_{1,42.2} = 0.2$	N.S.
	Songbirds, autumn	No difference	$F_{1,38} = 0.0$	N.S.

The table shows the effects on track direction of the interactions between angle α and different focal variables (left column) according to mixed GLMs with track direction as the dependent variable and angle α and the focal variable as covariate/fixed factors, along with the interaction between the variables, and with year as a random factor. Test statistics refers to the interaction effect of angle α * focal variable.


Spring
Autumn
Track
Heading
Downwind


A
Wind speed (m/s)
0
5
10
15
20
25
Songbirds autumn
Moths autumn
Songbirds spring
Moths spring
B
Ground speed (m/s)
0
10
20
30
Songbirds autumn
Moths autumn
Songbirds spring
Moths spring
C
Frequency
0
5
10
15
20
0.1
1
10
WS/AS (log scale)
Birds
Moths


Active downstream orientation
CBDO
Full drift
Partial compensation
Complete compensation
PDM
Heading
Track
α
β
δ
Flow
No slope
Slope >1
Slope = 1
Slope <1
Slope = 0


Spring
Autumn
Songbirds
Moths
Track (°)
α (°)
180
150
120
90
60
30
0
-30
-60
-90
-120
-150
-180
360
330
300
270
240
210
180
150
120
90
60
30
0
-120
-90
-60
-30
0
30
60
90
120