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Supplemental Information: Detection of flow direction in high-flying insect and songbird migrants

Jason W. Chapman, Cecilia Nilsson, Ka S. Lim, Johan Bäckman, Don R. Reynolds, Thomas Alerstam, and Andy M. Reynolds

Supplemental Tables

Table S1. 2-way ANOVA test statistics of the effect of wind direction and migration season on the size of the corrected offsets (δ_{CORR}) of *A. gamma* moths

Source	DF	Sum of Squares	Mean Square	<i>F</i> -value	P-value
Wind direction	1	3845	3845	11.58	<0.001
Season	1	515	515	1.55	0.217
Season x Direction	1	472	472	1.42	0.236
Residual	84	27,898	332		
Total	87	32,470			

Table S2. 2-way ANOVA test statistics of the effect of wind direction and migration season on the size of the corrected offsets (δ_{CORR}) of songbirds

Source	DF	Sum of Squares	Mean Square	<i>F</i> -value	P-value
Wind direction	1	0.36	0.36	0.00	0.987
Season	1	5315	5315	3.88	0.053
Season x Direction	1	103	103	0.08	0.785
Residual	75	102,784	1370		
Total	79	1,117,607			

Supplemental Figure

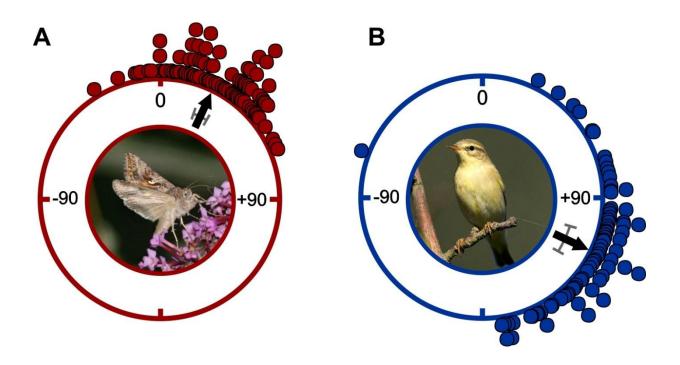


Figure S1. (A) Distribution of moth δ_{CORR} offsets when the angle between the flow and the PDM is large ($\omega > 25^{\circ}$). (B) Distribution of songbird δ_{CORR} offsets when the angle between the flow and the PDM is large ($\omega > 25^{\circ}$).

Supplemental Experimental Procedures

1. Entomological vertical-looking radar operating procedures

We analysed the relationship between flight heading and downwind direction in thousands of individual silver Y moths *Autographa gamma* engaged in spring and autumn high-altitude migratory flights. Data were collected by two specialised vertical-looking entomological radars (VLRs) 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. Data from the three locations was highly consistent and so was combined. Detailed description of the VLR equipment and operating procedures are published elsewhere [S1-3]. Briefly, individual targets flying within 15 defined altitude bands (45 m deep) arranged vertically above the radar (between 150–1188 m) are interrogated when they pass through the beam. The automated analysis procedure yields the horizontal speed, displacement direction (track), body alignment (flight heading), 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 [S4–S6]. We restricted analysis of radar-detected moths to a 2-hour period from 22:00 - 00:00 GMT and within a height range of 300-600 m above the ground so that wind vectors would be very similar for all individuals. Radar data was used to calculate the mean nightly values for insect flight heading and '*downwind offset*' δ , but only values from 'mass migration' nights (see "Statistical Analyses" below) were included in the analysis. Data from spring and autumn migration periods were combined for analysis. Wind data for the insect migration events was not directly measured, but was calculated from the radar-measured insect flight vectors (see section entitled "Directional variables and circular statistical procedures" below).

2. Ornithological tracking radar operating procedures

Nocturnal passerine migrants were recorded with X-band tracking radars in Lund and Falsterbo, south Sweden, during spring and autumn migration seasons between 1999 and 2011. Lund and Falsterbo data were highly consistent, and are therefore combined. All tracks were collected during a period of 4 hours either side of midnight (local time), when it was dark. 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. Only targets identified as single individual songbirds (indicated by the characteristic radar echo signature pattern associated with bounding flight typical of songbirds) were included in this study. Radar data was used to calculate the mean nightly values for songbird flight heading and '*downwind offset*'

 δ , but only values from 'mass migration' nights (see section entitled "Directional variables and circular statistical procedures" below) were included in the analysis. Data from spring and autumn migration periods were combined for analysis. Complete wind profiles were collected within 2 h of all bird tracks, by releasing and tracking with the radar helium balloons (carrying reflectors) from ground level up to 3000 m. The wind measurement at the mean altitude of each individual bird track was used in the analysis, with a maximum difference of 150m. Nocturnal songbird migrants passing over the radars in southern Sweden are likely able to see a large part of the surrounding landscape, which is mainly mixed urban and agricultural areas. There is also a prominent coast line that is probably available as a visual cue during the night, but most importantly there are also plenty of cites in the vicinity. The artificial light from the cities will be a reliable visual cue for the birds, even on very dark nights. The radar operating procedures and data handling have been described in detail elsewhere [S7, S8].

3. Directional variables and circular statistical procedures

The principal directional variables used in these analyses were as follows:

(i) Flight heading vector (the self-powered flying direction and airspeed)

For moths the VLR identifies the axis along which the insect's body is aligned, but this is a bidirectional value with a 180° ambiguity (i.e. it contains the real heading and the polar opposite of the heading). The correct flight heading is obtained by selecting the value which is closest to the migratory track (the movement direction of the moth relative to the ground), as previous work has shown that moths habitually fly close to the downwind direction, which will be similar to the track as wind speeds are considerably greater than the insect's selfpowered flight speed [S4–S6]. Silver Y moth airspeeds were not measured directly or calculated, but assumed to be a constant 4 m/s (see section entitled "Estimation of silver Y moth airspeeds" below). Songbird heading vectors (speed and direction) were calculated by subtraction of the wind vector (measured directly, see below) at the altitude where the bird was flying, from the bird's track and ground speed vector (measured directly by the tracking radar).

(ii) Flow vector (wind speed and the direction - towards which the wind is blowing)

For songbirds, flow vectors were measured within 2 h of all bird tracks, by releasing helium balloons carrying reflectors and tracking the speed and direction of their (windborne) progress at bird flight altitudes. The flow vectors for silver Y moth migrants were calculated by subtraction of the moth's heading vector (heading direction measured by the VLR, see above;

self-powered airspeed estimated at 4 m/s, see below) from the moth's track and ground speed vector (measured directly by the VLR).

(iii) Preferred Direction of Movement (PDM)

This term represents the direction towards which the migrants attempt to move during spring and autumn migrations, and has been previously estimated by us for each taxon in each season [S9] as follows: 353° for silver Y moths and 18° for songbirds during spring; 210° for silver Y moths and 214° for songbirds during autumn.

(iv) Downwind offset (δ)

This is the angle between the flight heading and the flow direction (see Figure 1 in the main paper). Insect flight headings are typically close to the downwind, and so for the silver Y moths it provides a measure of the degree to which they have offset their self-powered flight direction from the flow. Songbird flight directions are considerably less influenced by the wind, and so this variable is less relevant to birds than to insects.

(v) Angular deviation between the PDM and the flow (ω)

This is a measure of how far the flow will tend to deflect an individual's movement from its PDM. When ω is small (< 25°) the flow will only have a minor effect on the ability of an organism to fly along its PDM (especially for the faster flying songbirds), but when ω is large (> 25°) the flow will have a substantial effect on the ability to move along the PDM (especially for the slower flying moths).

These five variables were calculated for every individual moth and songbird recorded, and then means were calculated for each night included in the analysis. Only 'mass migration' nights were used in the analyses; this was achieved by restricting analysis to nights with 25 or more individual tracks. This resulted in 8,184 tracks on 118 nights for *A. gamma* moths (accounting for 78% of the total spring and autumn sample), and 4,178 tracks on 89 nights for songbirds (accounting for 83% of the total spring and autumn sample). The Rayleigh test of uniformity for circular data [S10] was used to calculate the nightly mean heading direction and flow direction for the combined datasets.

4. Estimation of silver Y moth airspeeds

It is not possible to directly measure the self-powered airspeed of the migrating silver Y moths with the entomological VLRs, and so we have used three independent methods to obtain a reliable estimate of their airspeed.

Firstly, we used reports in the literature of airspeeds of noctuid moths similar in size to *A*. *gamma* and migrating at high altitude, which were estimated by tracking migrating moths and windborne balloons with radar, and subtracting one vector from the other. Two such studies produced estimated mean values of 4.5 m/s for *Helicoverpa zea* migrating above Texas [S11], and 3.5 m/s for a variety of noctuid moths (including *H. punctigera, Persectania ewingii* and *Agrotis munda*) migrating across the Bass Strait between southern Australia and Tasmania [S12]. We therefore assumed that a mean value of 4 m/s would be a realistic estimate for *A. gamma* based on these previous estimates.

Secondly, we used the general relationship between mean self-powered airspeed and body size of insects produced by Lewis and Taylor [S13], repeated as Fig. 24 on page 92 of Johnson 1969 [S14]. Body size is defined as wingspan x body length, and we calculated this figure to be 680 mm² for *A. gamma* (based on a mean wingspan of 37.8 mm, derived from measurements of 10 *A. gamma* caught in light traps at Rothamsted; and a body length of 18 mm, measured from life-size photographs reproduced in Skinner [S15]). Using Lewis and Taylor's relationship, a body size of 680 mm² produces an airspeed of ~4 m/s.

Thirdly, Prof Colin Pennycuick used his "Bird Flight Performance" program [S16], which can be found online (<u>http://nhsbig.inhs.uiuc.edu/wes/pennycuick.html</u>), to estimate the 'minimum power speed' (U_{mp}) for *A. gamma* based on our size estimates. U_{mp} is the airspeed of a flying animal that will maximise the time spent airborne for a given amount of fuel [S17], and thus the airspeed that may be expected for an insect migrating on favourably-directed winds which are much faster than its airspeed (as is the case for *A. gamma*, where typical wind speeds experienced during migration are three or four times faster than its airspeed [S9]). This method produced a value of 3.80 m/s for U_{mp}, which is very similar to the first two methods.

We therefore used a mean airspeed of 4 m/s for migrating *A. gamma* moths in our calculations of the flow vectors.

Supplemental References

- S1. Drake, V.A., and Reynolds, D.R. (2012). *Radar Entomology: Observing Insect Flight and Migration*. CABI, Oxfordshire, UK.
- S2. Chapman, J.W., Smith, A.D., Woiwod, I.P., Reynolds, D.R., and Riley, J.R. (2002). Development of vertical-looking radar technology for monitoring insect migration. Comput. Electron. *Agric. 35*, 95–110.
- S3. Chapman, J.W., Drake, V.A., and Reynolds, D.R. (2011). Recent insights from radar studies of insect flight. Annu. Rev. Entomol. 56, 337–356.
- S4. Chapman, J.W., Reynolds, D.R., Mouritsen, H., Hill, J.K., Riley, J.R., Sivell, D. *et al.* (2008).
 Wind selection and drift compensation optimize migratory pathways in a highflying moth. Curr. Biol. *18*, 514–518.
- S5. Chapman, J.W., Nesbit, R.L., Burgin, L.E., Reynolds, D.R., Smith, A.D., Middleton, D.R., and Hill, J.K. (2010). Flight orientation behaviors promote optimal migration trajectories in high-flying insects. Science, 327, 682–685.
- S6. Alerstam, T., Chapman, J.W., Bäckman, J., Smith, A.D., Karlsson, H., Nilsson, C. *et al.* (2011). Convergent patterns of long-distance nocturnal migration in noctuid moths and passerine birds. Proc. Roy. Soc. B *278*, 3074–3080.
- S7. Bäckman, J., and Alerstam, T. (2003). Orientation scatter of free-flying nocturnal passerine migrants: components and causes. Anim. Behav. 65, 987–996.
- S8. Karlsson, H., Nilsson, C., Bäckman, J., and Alerstam, T. (2012). Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. Anim. Behav. *83*, 87–93.
- S9. Chapman, J.W., Nilsson, C., Lim, K.S., Bäckman, J., Reynolds, D.R., and Alerstam, T. (2015). Adaptive strategies in nocturnally migrating insects and songbirds: contrasting responses to wind. J. Anim. Ecol. (in press).
- S10. Fisher, N.I. (1993). *Statistical Analysis of Circular Data*. Cambridge University Press, Cambridge.
- S11. Westbrook, J.K., Wolf, W.W., Lingren, P.D., and Raulston, J.R. (1994). Flight speed and heading of migrating corn earworm moths relative to drifting tetroons. Proceedings of 21st Conference on Agricultural and Forest Meteorology - 11th Conference on Biometeorology, March 7-11 1994, San Diego, California, pp. 423426. American Meteorological Society, Boston.
- S12. Drake, V.A., Helm, K.F., and Readshaw, J.L. (1981). Insect migration across Bass Strait during spring: a radar study. Bull. Ent. Res. *71*, 449–446.

- S13. Lewis, T., and Taylor, L.R.(1967). *Introduction to Experimental Ecology*. Academic Press, London & New York.
- S14. Johnson, C.G.(1969). *Migration and Dispersal of Insects by Flight*. Methuen & Co Ltd, London.
- S15. Skinner, B. (2009). Colour Identification Guide to Moths of the British Isles. Apollo Books, Denmark.
- S16. Pennycuick, C.J. (1989). *Bird Flight Performance: a Practical Calculation Manual*. Oxford University Press, New York.
- S17. Hedenström, A., Bowlin, M.S., Nathan, N., Nolet, B.A., and Wikelski, M. (2011). Mechanistic principles of locomotion performance in migrating animals. In: *Animal Migration: a Synthesis* (eds: Milner-Gulland, E.J., Fryxell J.M., and Sinclair, A.R.E.). Oxford University Press, Oxford.