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

Jason W. Chapman[1,2,†,*], Cecilia Nilsson[3,†], Ka S. Lim[1], Johan Bäckman[3], Don R. Reynolds[1,4], Thomas Alerstam[3], and Andy M. Reynolds[1]

Goal-oriented migrants travelling through the sea or air must cope with the effect of cross-flows during their journeys if they are to reach their destination [1–3]. In order to counteract flow-induced drift from their preferred course, migrants must detect the mean flow direction, and integrate this information with output from their internal compass, to compensate for the deflection. Animals can potentially sense flow direction by two nonexclusive mechanisms: either (i) *indirectly*, by visually assessing the effect of the current on their movement direction relative to the ground; or (ii) *directly*, via intrinsic properties of the current [4]. Here, we report the first evidence that nocturnal compass-guided insect migrants use a turbulence-mediated mechanism for directly assessing the wind direction 100s m above the ground. By comparison, we find that nocturnally-migrating songbirds do not use turbulence to detect the flow; instead they rely on visual assessment of wind-induced drift to indirectly infer the flow direction.

Billions of insects and songbirds carry out compass-guided nocturnal migrations between Europe and Africa by flying in high-altitude airstreams [5,6], where they must cope with unfavourably-directed flows. The mechanisms by which these two taxa, differing

substantially in flight performance and sensory capabilities, detect flow direction while flying high above the ground at night have eluded discovery. We answer this question by carrying out a comparative analysis of >10,000 radar tracks of individually migrating noctuid moths (*Autographa gamma*) and songbirds, and associated wind vectors, during multiple spring and autumn migrations over north-western Europe (see Supplemental Experimental Procedures).

Fluid-dynamic theory [4] posits that fine-scale turbulence is anisotropic (i.e. not equal in all directions), and stronger in the downstream direction. Thus if a flying animal can detect these weak turbulent fluctuations it can identify the flow direction. Crucially, the theory predicts that due to the Ekman spiral, an animal attempting to align it's heading with the mean flow will tend to misalign slightly to the right of the downstream in the Northern Hemisphere (and to the left in the Southern Hemisphere) [4]. To determine if *A. gamma* moths and songbirds use these anisotropic turbulence cues to detect the flow direction, we analysed distributions of the '*downwind offset*' δ (the angle between the self-propelled flight heading and the downwind direction; Figure 1), in relation to the taxon-specific seasonal *preferred direction of movement* (PDM) of both taxa [6] (see Supplemental Experimental Procedures). We modified the absolute values of δ in two ways. Firstly, we calculated the '*corrected downwind offset*' δ_{CORR}, by assigning a positive value if the heading corrected for wind-induced drift (i.e. the heading was closer to the PDM than the flow was; Figure 1A), but a negative value if the heading increased the drift (i.e. it was further away; Figure 1B). Secondly, we calculated the '*turbulence downwind offset*' δ_{TURB}, by assigning a positive value if the offset matched the prediction of the fluid-dynamic theory (i.e. the heading was to the right of the flow; Figure 1B) and a negative value if it did not match the theory (i.e. heading to the left of the flow; Figure 1A).

On occasions when the airflow was close to the seasonal PDM (i.e. the angle ω between the flow and PDM was < 25°) the distribution of δ_{CORR} for *A. gamma* moths was not significantly different from zero (n = 30 migration events, δ_{CORR} = +2.3°, 95% CI = ±6.6°; Figure 1C), indicating that moths did not correct for small amounts of drift when travelling

close to their preferred direction, and on average flew downwind. However, the distribution of δ_{TURB} was significantly different from the expected value of zero and skewed to the right (n = 30, δ_{TURB} = +8.6°, 95% CI = ±5.8°; Figure 1D), in line with the predictions of the turbulence mechanism of flow detection. In the few cases where the downwind direction for the songbirds was close to their seasonal PDM, the distribution of both δ_{CORR} and δ_{TURB} was centred around zero and was not significantly skewed towards either the PDM or the right (n = 10, δ_{CORR} = -2.9°, 95% CI = ±20.1°, Figure 1E; δ_{TURB} = -3.5°, 95% CI = ±20.0°, Figure 1F).

When downwind directions were further away from the seasonal PDM (i.e. ω > 25°) then offsets were consistent with both groups partially correcting for drift (moths: n = 88, δ_{CORR} = +25.9°, 95% CI = ±4.0°, P < 0.001, Figure S1A; songbirds: n = 79, δ_{CORR} = +115.9°, 95% CI = ±7.6°, Figure S1B), as previously reported [6,7]. However, a strong signal of turbulence-induced offsets was visible in the moth drift corrections, as offsets were considerably larger when the flow direction was to the left of the PDM (when turbulence-induced offsets and drift corrections would both be on the right and thus additive), than when the flow was to the right of the PDM (when turbulence-induced offsets and drift corrections would oppose each other); this difference was significant (2-way ANOVA, effect of flow direction: $F_{1,84}$ = 11.6, P < 0.001, Figure 1G, Table S1). By contrast, in songbirds the offset between heading and flow was not significantly different in winds blowing from the left or right of the PDM ($F_{1,75}$ = 0.00, P = 0.987, Figure 1H, Table S2), showing no signal of turbulence-induced offsets.

These results clearly indicate that *A. gamma* moths integrate directional information from two separate sensory capacities – direct detection of the flow direction via turbulence cues and detection of their preferred migration direction via a compass mechanism – and then adopt optimal flight headings. This is the first evidence of such a capability in aerial or marine animal migrants, but given that organisms as diverse as jellyfish [8], copepods and other zooplankton [9], and juvenile sea turtles [10] have also been postulated to directly detect currents, such sensory capabilities may prove to be widespread across the animal kingdom. However, our results indicate that nocturnally-migrating songbirds do not directly detect currents via turbulence cues; instead they probably rely on visual assessment of their

movement relative to ground features to compensate for drift. In the study region (southern Sweden), migrating songbirds will be able to see a variety of landscape features including a prominent coastline and artificial light from several large cities in the immediate area, and these ground features presumably provide reliable references against which it is possible for songbirds to assess the degree of crosswind drift. Given the sensitivity of nocturnal insect vision, we also expect that highflying moth migrants are able to perceive some coarse landscape features, particularly under bright moonlight/starlight conditions. However, if moths use an optomotor-type mechanism for detecting their movement direction relative to the ground, we would not expect to observe any directional bias in the distribution of downwind offsets. We therefore conclude that the turbulence mechanism overrides any visually-guided mechanism of flow detection, but we do not completely rule out a role for vision and this topic would repay further study.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two tables and one figure and can be found with this article online at

 http://dx.doi.org/10.1016/j.cub.2015.07.074.

References

1. Chapman, J.W., Klaassen, R.H.G., Drake, V.A., Fossette, S., Hays, G.C., Metcalfe, J.D., Reynolds, A.M., Reynolds, D.R., and Alerstam, T. (2011). Animal orientation strategies for movement in flows. Curr. Biol. *21*, R861–R870.

2. Hays, G.C., Christensen, A., Fossette, S., Schofield, G., Talbot, J. & Mariani, P. (2014). Route optimisation and solving Zermelo's navigation problem during long distance migration in cross flows. Ecol. Lett. *17*, 137–143.

3. McLaren, J.D., Shamoun-Baranes, J., Dokter, A.M., Klaassen, R.H.G., and Bouten, W. (2014). Optimal orientation in flows: providing a benchmark for animal movement strategies. J. Roy. Soc. Interface, *11*, 20140588.

4. Reynolds, A.M., Reynolds, D.R., Smith, A.D., and Chapman, J.W. (2010). A single wind-mediated mechanism explains high-altitude 'non-goal oriented' headings and layering of nocturnally-migrating insects. Proc. Biol. Sci. *277*, 765–772.

5. Chapman, J.W., Reynolds, D.R., and Wilson, K. (2015). Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. Ecol. Lett. *18*, 287–302.

6. 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).

7. Chapman, J.W., Reynolds, D.R., Hill, J.K., Sivell, D., Smith, A.D., and Woiwod, I.P. (2008). A seasonal switch in compass orientation in a high-flying migratory moth. Curr. Biol. *18*, R908–R909.

8. Fossette, S., Gleiss, A.C., Chalumeau, J., Bastian, T., Armstrong, C.D., Vandenabeele, S.. Karpytchev, M., and Hays, G.C. (2015). Current-oriented swimming by jellyfish in the absence of a fixed reference frame and the role in bloom maintenance. Curr. Biol. *25*, 342–347.

9. Genin, A., Jaffe, J.S., Reef, R., Richter, C., and Franks, P.J. (2005). Swimming against the flow: a mechanism of zooplankton aggregation. Science *308*, 860–862.

10. Kobayashi, D.R., Farman, R., Polovina, J.J., Parker, D.M., Rice, M., Balazs, H. (2014). "Going with the flow" or not: evidence of positive rheotaxis in oceanic juvenile loggerhead turtles (*Caretta caretta*) in the South Pacific Ocean using satellite tags and ocean circulation data. PLoS ONE *9*, e103701.

[1]Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK

[2]Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall, TR10 9EZ, UK

[3]Department of Biology, Lund University, SE-223 62 Lund, Sweden

[4]Natural Resources Institute, University of Greenwich, Chatham, Kent, ME4 4TB, UK

†These authors contributed equally.
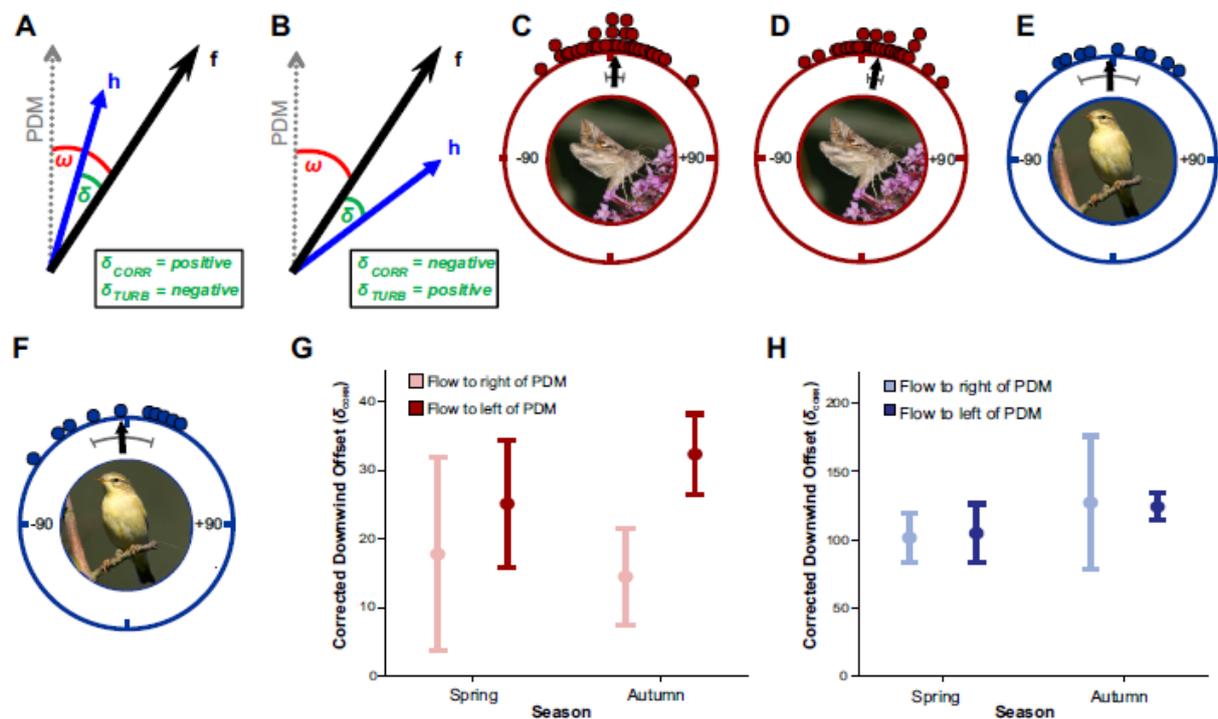
*Correspondence: jason.chapman@rothamsted.ac.uk

Figure Legend

Figure 1. Evidence for direct flow detection in nocturnally-migrating moths

(A) Schematic diagram of moth and songbird heading (h) and flow (f) directions during spring in relation to the seasonal preferred direction of movement (PDM) which is assumed to be due north in this schematic; ω is the angle between PDM and flow, δ is the angle between flow and heading. The angle δ would be positive if considering correction for drift (δ_{CORR}) but negative (to the left) if considering the turbulence mechanism (δ_{TURB}). (B) Same as (A), but here the heading is on the other side of the flow with respect to the PDM, and thus δ_{CORR} would be negative but δ_{TURB} would be positive. (C) Distribution of moth δ_{CORR} offsets when the angle between the flow and the PDM is small ($\omega < 25°$). Each of the small coloured circles on the periphery of the plot represents the mean value for a single migration night (spring and autumn datasets combined), while the overall mean offset is shown by the black arrow with grey bars representing the 95% CI. (D) Distribution of moth δ_{TURB} offsets when the

angle between the flow and the PDM is small ($\omega < 25°$). (E) Distribution of songbird δ_{CORR} offsets when the angle between the flow and the PDM is small ($\omega < 25°$). (F) Distribution of songbird δ_{TURB} offsets when the angle between the flow and the PDM is small ($\omega < 25°$). (G) Seasonal patterns of the mean (±95% CI) of moth δ_{CORR} offsets when the angle between the flow and the PDM is large ($\omega > 25°$), in flows to the right and to the left of the PDM (in spring: n = 11 to the right and n = 18 to the left; in autumn: n = 16 to the right and n = 43 to the left). (H) Seasonal patterns of the mean (±95% CI) of songbird δ_{CORR} offsets when the angle between the flow and the PDM is large ($\omega > 25°$), in flows to the right and to the left of the PDM (in spring: n = 27 to the right and n = 15 to the left; in autumn n = 4 to the right and n = 33 to the left).

Figure 1

Supplemental Information

Document S1. Supplemental Experimental Procedures, two tables and one figure.

http://www.cell.com/cms/attachment/2035558669/2051159039/mmc1.pdf