Correspondence

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

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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 *indirectly*, by visually assessing the effect of the current on their movement direction relative to the ground; or *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 hundreds of metres 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 — that is, 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 its 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 (that is, the heading was closer to the PDM than the flow was; Figure 1A), but a negative value if the heading increased the drift (that is, 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 (that is, the heading was to the right of the flow; Figure 1B) and a negative value if it did not match the theory (that is, 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 (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 (two-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.

Supplemental Information

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

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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.

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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).

Supplemental Information

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

In Brief:

Flying and swimming migrants need to detect the effect of flows on their movement. Chapman *et al*. report that high-flying nocturnal moth migrants use micro-turbulence cues to directly detect the wind direction, whereas nocturnal songbird migrants seemingly detect the flow indirectly by visual assessment of their drift in relation to the ground.