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Compensation for wind drift by bumble-bees

In his classic studies on honeybee navigation, von Frisch had to rely on qualitative visual observations of the bees' flight paths, but nevertheless reached the surprising conclusion that bees seem to anticipate lateral wind drift and compensate by flying in shallow curves on the upwind side of their intended tracks^{1,2}. We have investigated wind compensation^{1–3} with much greater precision by using radar^{4,5} to record the flight trajectories of individual bumble-bees (*Bombus terrestris* L.) foraging over arable farmland⁶. Flights typically covered distances of 200 to 700 metres, but bees maintained direct routes between the forage areas and their nests, even in winds with a strong cross-track component. Some bees overcompensated slightly, as described by von Frisch, but most stayed on course by heading partly into the wind and moving obliquely over the ground.

How did the bumble-bees know how far to turn off course to achieve the correct track to their destinations? Several species of Hymenoptera are known to use a Sun compass for navigation^{1,8}, and if, as seems likely, bumble-bees share this ability⁹, we propose that a simple strategy to keep on track in cross-winds would be for them to adjust their headings until the direction of ground image movement over their retinæ (the optical flow¹⁰) occurred at the angle relative to the Sun's azimuth that corresponded to their intended tracks. This mechanism of controlling track direction by direct comparison of two optical directional cues not subject to parallax does not require the bees to assess wind speed or direction, or to compute the combination of heading and air speed required to stay on track. Support for a mechanism based on optical flow comes from visual observations that honeybees flying over water begin to drift with the wind¹¹.

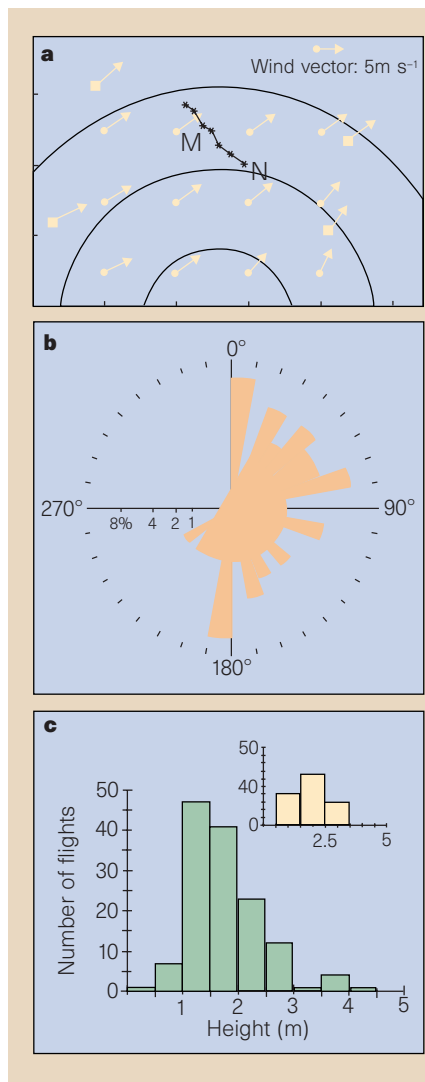


Figure 1a shows an example of cross-wind flight compensation behaviour, which was typical of the 53 return flights examined (Fig. 1b). In still air (where air speed is the same as ground speed), the mean air speed of foragers was $7.1 \pm 0.43 \text{ m s}^{-1}$ ($n=8$), and they flew about 2 m above the ground. In windier conditions, they flew lower on slow upwind tracks and higher in faster downwind movements (Fig. 1c, inset), as though they were adjusting their heights of flight to maintain a preferred rate of optical flow. Results from still air indicate that, if this were the case, the preferred rate for the visual field directly beneath the bees was about $7 \text{ m s}^{-1}/2 \text{ m} = 3.5 \text{ rad s}^{-1}$. We therefore used this value to estimate the height of each flight (Fig. 1c), and subtracted the wind vector at this height from the bees' ground vector to yield air speed and heading.

The overall average air speed found in this way was $7.3 \pm 1.2 \text{ m s}^{-1}$ (s.d.) ($n=74$) in June, and $6.2 \pm 1.2 \text{ m s}^{-1}$ ($n=63$) for July and August, and upwind flight was about 1 m s^{-1} faster than downwind flight in both study periods. The average air speed for June was greater than the fastest air speed (7 m s^{-1}) predicted for bumble-bee

workers, implying a power output exceeding the 180 W kg^{-1} maximum currently attributed to bee flight muscle¹³.
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