

Table 1. The orientation behaviour of large insect migrants in the ‘transmigration’ phase (i.e. main period of migratory flight, after the initial ascent to altitude and before the descent/ landing phase).

<p>A: Night-flying migrants. Nocturnal transmigration (at least in fair weather) is adapted to prolonged periods of steady flight, with insects distributed independently of each other, and maintaining relatively constant altitudes in the stably-stratified, close-to-geostrophic airflows (Drake & Reynolds 2012). Changes in displacement speed and direction, and in heading direction, tend to be gradual, except where migrants are subject to transient atmospheric disturbances such as convergence lines (e.g. sea-breeze fronts, storm outflows) or gravity waves (Drake & Reynolds 2012). Fast displacements can occur due to high wind speeds, especially in super-geostrophic ‘low-level jets’. Other advantages of nocturnal migration include avoidance of thermal stress in warm climes, reduction in overheating due to metabolic heat generated by continuous wing-flapping, and avoidance of day-active predators.</p>		
Orientation strategy	Comments on mechanisms and cues	Function; advantages and disadvantages
<p><i>Random headings:</i></p> <ul style="list-style-type: none"> occurs in some <i>small</i> insect migrants such as the brown planthopper (Riley et al. 1991); unusual in large high-altitude insect migrants. 	<p>Apparent examples detected by radar may be the result of :</p> <ul style="list-style-type: none"> an assortment of species with differing ‘preferred inherited directions’ (see below); temporary disruption of headings due to mesoscale disturbances/windshift lines (Drake & Reynolds 2012); appropriate direction cues may be temporarily absent; for example, if orientation is maintained by some intrinsic property of the wind, such as turbulent velocity and acceleration cues (Reynolds et al. 2010a,b), these cues may be infrequent or weak or too isotropic to be useful. 	<ul style="list-style-type: none"> Random headings act so as to increase population dispersal during migration, May reflect the absence of suitable orientation cues, or sensory modalities in the species concerned. <i>However</i>, small insects make virtually no contribution to their ground speed at altitude, so there may be little adaptive benefit maintaining a particular heading.
<p><i>Wind-related orientation:</i></p> <p>i) <i>Active downwind heading</i> –</p> <ul style="list-style-type: none"> occurs in moderate-sized and some large migrants. 	<ul style="list-style-type: none"> Occurrences of wind-related orientation are more convincing if migrants tend to <i>maintain</i> an orientation close to downwind despite changes in wind direction with altitude and/or with time. The wind direction could be determined by visual perception of the apparent movement of the ground, but in some cases at least, an optomotor-type mechanism seems unlikely (see Reynolds et al. 2010a), and orientation appears to be maintained by some intrinsic feature of the wind. Sometimes orientations are closely related to the downwind direction but offset to one side of the wind-line by a small amount, typically $\sim 20^\circ$ (Reynolds et al. 2010a). This bias may 	<p>The migrant’s airspeed is added to the wind speed, thus maximizing the distance covered in a given time. Good energy-saving strategy if:</p> <ol style="list-style-type: none"> favourable habitats do not lie in any particular compass direction (but the tactic could be combined with selective flight on winds from appropriate direction to achieve directed movements); in arid environments, where long-range downwind movement is particularly advantageous because it takes migrants (e.g. solitary locusts, armyworm moths) towards atmospheric convergences zones (e.g. ITCZ) where rain is likely to fall.

	indicate the type of turbulence cue being used to maintain the orientation (see main text).	
<p><i>Wind-related orientation:</i></p> <p>ii) <i>With large off-wind headings</i></p> <ul style="list-style-type: none"> rather unusual 	<ul style="list-style-type: none"> Occasionally, wind-related orientations are observed with larger off-wind headings, which nonetheless do <i>not</i> seem to accord with a strategy of Compass-Biased Downstream Orientation (see next category below); Orientations are mysterious – may be caused by the absence of suitable orientation cues, or an unadaptive misinterpretation of available cues. 	Not clear.
<p><i>Compass-biased Downwind Orientation:</i></p> <ul style="list-style-type: none"> heading deviates somewhat from downwind so that it lies between the downwind direction and a ‘preferred inherited direction’ (Chapman et al. 2011b); occurs in some long-range migrant moths, in particular <i>Autographa gamma</i> (Silver-Y moth). 	<ul style="list-style-type: none"> Strategy requires that migrants orientate with respect to the wind <i>and</i> have a compass sense in order to take up their ‘preferred inherited direction’ (Chapman et al. 2008a,b). Migration does not occur to any extent in winds blowing in highly unfavourable directions, although a precise point at which migratory flights are aborted is not clear (e.g. before take-off, or after a short exploratory flight). When moths reach migration altitudes (often at the height of the fastest winds), they adopt headings that partially counteract crosswind drift, but only if the drift angle exceeds ~20°. The basis of the compass sense is unknown – it could be magnetic. There is a seasonal reversal of preferred directions between spring and autumn (Chapman et al. 2008b, 2013). 	<ul style="list-style-type: none"> <i>Compass-biased Downwind Orientation</i> appears to be a trade-off between moving rapidly and moving in the ‘preferred inherited direction’. In the case of the southward movement of <i>A. gamma</i>, the strategy results in migration trajectories that were significantly longer, and closer to the seasonally preferred direction, than would be achieved by merely drifting downwind (Chapman et al. 2010).
<p>B: Day-flying migrants.</p> <p>Large day-flying migrants such as butterflies are largely ‘ectothermic’, relying on various sun-basking behaviours to raise thoracic temperature in suboptimal conditions, and this precludes nocturnal migration.</p> <p>Migrants have to contend with turbulence due to thermal convection, and maintenance of a reasonably consistent cruising speed and orientation through the convection field is arduous. (That convection has a strong effect is shown by the extreme spatial heterogeneity seen in such migrants observed on scanning radars (Drake & Reynolds 2012)).</p> <p>Migrants, like the monarch butterfly (<i>D. plexippus</i>), which soar extensively on convective updraughts evidently have to fly in the day.</p> <p>Migrants are exposed to day-active predators (e.g. dragonflies eaten by co-migrant birds-see main text).</p>		
<p><i>Migration within flight boundary layer (FBL)*:</i></p> <ul style="list-style-type: none"> the only type of insect 	<ul style="list-style-type: none"> Uses a solar compass (based on sun’s azimuth and/or sun-linked patterns of light intensity or polarization) which may or may not be time-compensated. 	<ul style="list-style-type: none"> Seasonal migrations can take place in ‘preferred inherited directions’ largely independent of the wind direction.

<p>migration which is easily visible (when intense) by humans, so there are anecdotal reports throughout the ages.</p>	<ul style="list-style-type: none"> • This is combined with an assessment of drift from ground image movement over the insect retina (optic flow) – if the degree of drift is unacceptable, this may be reduced by alterations in flight direction or direction. • Compensation for crosswind drift varies considerably between taxa (Srygley & Dudley 2008). • FBL migrants sometimes also utilise visual pilotage along linear ‘leading lines’ (e.g. coastlines, roads) as long as these are compatible with ambient wind velocity and any preferred inherited direction. 	<ul style="list-style-type: none"> ○ Progress will be rather slow, but the risk of perilous drift over unsuitable areas may be reduced. ○ Interspersing of migration and feeding/oviposition bouts is practicable as the low altitude flight facilitates encounters with host plants. ○ The major disadvantage would seem to be the high energy expenditure, particularly if moving against a headwind.
<p><i>Daytime migration above the flight boundary layer:</i> <i>i) approximately downwind heading and relatively continuous powered flight.</i></p> <ul style="list-style-type: none"> • apparently characteristic of the painted lady, <i>Vanessa cardui</i> under some circumstances (Stefanescu et al. 2007; Chapman et al. 2010). 	<ul style="list-style-type: none"> • Migrant’s displacement direction presumably assessed (by means of a solar compass combined with an inherited preferred direction). • If displacement is seasonally appropriate, there is continued ascent to high altitudes; if not, descent back into the FBL. 	<ul style="list-style-type: none"> ○ Allows much faster displacement of day-flying migrants than ‘within-FBL’ movement, or the “ascend on updraughts, then glide” strategy.
<p><i>ii) ascent on thermal updraughts or by mean of ‘slope lift’, then gliding across country.</i></p> <ul style="list-style-type: none"> • characteristic of the butterflies <i>D. plexippus</i> and <i>Nymphalis antiopa</i> (Camberwell beauty) and the dragonfly <i>Pantella flavescens</i>, under appropriate weather conditions. 	<ul style="list-style-type: none"> • Must be able to detect and exploit rising air, e.g. cease flapping flight in updraughts (and turn back at boundary of the ascending air?). • Must assess whether the displacement direction during the cross-country glide phase approximates to the seasonally favourable direction (as determined by means of a solar compass). • In the case of the Monarch there are apparently differing reactions to crosswinds from the left as opposed to from the right of the preferred (goal) direction (Gibo 1986). 	<ul style="list-style-type: none"> ○ Allows great energy saving, but with greater risk of drift than with FBL migration. (The thermals themselves drift downwind and it may be more difficult for the soaring migrant to monitor, from high altitude, whether they are being carried over unsuitable terrain.)

*The ‘flight boundary layer’ is the layer of air, extending a variable distance up from the ground, where the ambient wind speed is lower than the insect’s self-propelled flight speed.