Animal Orientation Strategies for Movement in Flows

Review

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For organisms that fly or swim, movement results from the combined effects of the moving medium — air or water — and the organism's own locomotion. For larger organisms, propulsion contributes significantly to progress but the flow usually still provides significant opposition or assistance, or produces lateral displacement ('drift'). Animals show a range of responses to flows, depending on the direction of the flow relative to their preferred direction, the speed of the flow relative to their own self-propelled speed, the incidence of flows in different directions and the proportion of the journey remaining. We here present a classification of responses based on the direction of the resulting movement relative to flow and preferred direction, which is applicable to a range of taxa and environments. The responses adopted in particular circumstances are related to the organisms' locomotory and sensory capacities and the environmental cues available. Advances in biologging technologies and particle tracking models are now providing a wealth of data, which often demonstrate a striking level of convergence in the strategies that very different animals living in very different environments employ when moving in a flow.

Introduction

The movement of individual animals from one place to another is a fundamental feature of life that impacts on virtually all aspects of animal ecology and population dynamics [1,2]. In the case of swimming and flying animals, movement can be significantly affected by the motion of the fluid — water or air — in which they are immersed. Animals that engage in goal-oriented flying or swimming movements can therefore be expected to have evolved mechanisms for identifying and exploiting favourably-directed flows, and coping with opposing ones [1–4]. The use of radar has been instrumental for developing an understanding of orientation behaviour in relation to winds among birds and insects [5,6] since the initial ornithological radar studies by pioneers

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such as David Lack [7]. More recently, advances in biologging technology [8] — the use of miniaturised tags for logging an animal's movements — and trajectory simulation [9–11] have provided a new impetus to this field. In this review, we focus on movements towards a specific point or broad-area goal (mainly migratory and homing movements over long distances) by actively swimming and flying animals (Figure 1; Box 1).

Orientation Responses and Strategies of Animals Moving in Flows

Animals can adapt to flows by employing two different, but not mutually exclusive, types of response: first, they can move at times, and at flight-altitudes or swimming-depths, so as to coincide with flows that are most favourable for movement in their preferred direction; second, they can orientate in relation to the flow such that they compensate for any drift away from their goal or maximise the distance covered. Of course, for animals with negligible locomotory speed through the medium, only the first type of response is possible (Figure 2). However, it is becoming increasingly clear that mechanisms for sensing flow direction, and strategies of adaptive orientation with respect to the flow direction, are not restricted to fast-moving animals [12–15], but are also present in organisms that have relatively limited capacities for counteracting the flow, such as large moths [9] and immature fish [16]. Responses involving a change in speed may also occur in some species, and a bird, for instance, is predicted to compensate for wind drift in an optimal way by adapting both heading direction and airspeed in relation to the wind [17]. However, it is still unknown if and to what degree such speed changes occur, and as the orientation behaviour defines the main type of response, we will not consider possible accompanying changes in locomotory speeds further.

Animals can orient themselves in a flow in a number of ways, and we distinguish here eight categories of orientation relative to the flow direction (Figure 3). The most basic response we recognise is passive downstream transport (Figure 3A), which occurs in organisms or propagules without self-propelled motion. The seven remaining categories involve active swimming or flying and represent a continuum of orientation responses from down-flow movement to heading into the flow (Figure 3B–H). Some of the responses (Figure 3C–G) imply that the organism has a preferred goal direction, and thus some navigational ability [18–20]. With two exceptions (Figure 3A,D), all responses imply that the animal can determine the flow direction either directly or indirectly (Box 2).

The optimal orientation response for an animal in a particular flow may change as the animal's journey progresses. Changes of flow from favourable to contrary (and vice versa), storms, drift towards hazardous regions, and depletion of energy reserves are all events that may require a changed response. When an animal's journey has a highly localised goal, responses can be expected to change as the destination is approached. The set of responses the animal adopts along its journey constitutes its 'orientation strategy' for
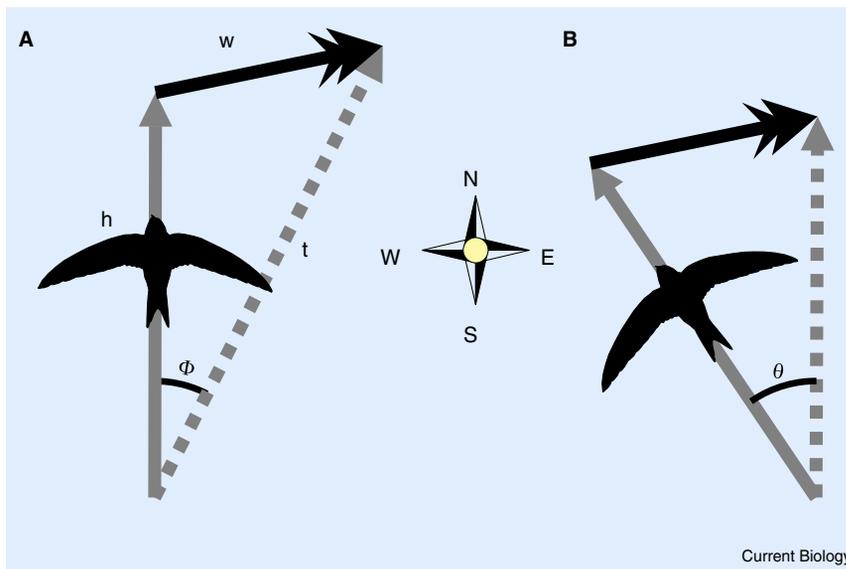
Figure 1. Triangles of velocities representing the flight of a bird.

(A) The bird is heading northwards with a certain airspeed (vector h) while the wind (vector w: wind direction and speed) is blowing almost eastwards. The bird's resulting movement approximately to the northeast (vector t: track and ground speed) is the vectorial sum of h and w. The bird is said to be experiencing drift through an angle Φ (the drift angle). (B) If the bird's preferred direction is northwards, in order to achieve movement in this direction it will have to adopt a heading that is directed somewhat into the wind. It is then said to be compensating, through an angle θ (the compensation angle). In this example, as the flow is nearly lateral to the preferred direction, it provides almost no *transport* but nor is it unfavourable in the sense of being *contrary*. Note that the bird travels further, and gets further north, by tolerating drift (A) than by compensating for it (B).

that journey. Such strategies are amenable to theoretical analysis. It has been shown, for example, that an animal migrating under variable flow conditions along the route should always aim to minimize the remaining distance to the goal after each migratory step [21]. This implies that, if the flow direction changes during the course of the journey, the animal should allow itself to be drifted initially but compensate for drift more and more the closer it gets to its destination. If the flow is constant throughout the journey, continuous full compensation (Figure 1B) is the theoretically optimal behaviour for animals travelling to a precise goal [21]. When the animal is seeking only to reach a broad region, and the distance is short in comparison with the scale of major flow regimes, strategies may be much simpler – perhaps no more than unvarying adoption of one of the response categories (Figure 3). Even for journeys with a precise goal, an unvarying response may be appropriate during all but the terminal phase of the journey and can be regarded as the strategy adopted for the journey's initial stages. Animals with no self-propelled speed inevitably have an unvarying strategy as only passive downstream transport is available to them. The mechanisms that animals use for orienting in relation to moving fluids are discussed in Box 2.

Passive Downstream Transport

This strategy (Figure 3A) is used by animals that are incapable of self-propelled locomotion and thus are unable to influence their speed and direction. The speed and direction of movement is essentially the same as the flow speed and direction, and thus such organisms are incapable of compensating for drift. There are close parallels between the dispersal of passively-transported animals and the long-distance dispersal of fungal spores, pollen and plant seeds [22]. The processes of passive downstream transport in animals have been studied most thoroughly in three groups of terrestrial arthropods — spiders, spider mites and moth caterpillars — which have independently evolved the use of secreted silken draglines for dispersal by 'ballooning' on the wind [23]. Other minute wingless arthropods (e.g. scale-insect 'crawlers' and some mites) do not

use silk threads but rely on small body size, dorso-ventral flattening of the body, long setae, and in some cases the production of wax filaments [24] to reduce their fall speeds.

All these organisms do, however, control when and where to launch themselves, often relying on specialized behaviours to enter the air-column. The selection of optimal conditions for take-off can result in wingless arthropods achieving extremely long-distance passive transport of the order of hundreds of kilometres [25], and thus it is a very efficient system for large-scale spatial redistribution. In a similar manner, small terrestrial arthropods (e.g. mites and Collembola) can travel considerable distances (up to several hundred kilometres) by sea-surface (pleuston) transport [26].

The transport of very slow-moving but actively swimming or flying organisms within flows, such as zooplankton in the marine environment, and micro-insects high in the atmospheric boundary layer, is regarded here as a form of passive downstream transport too. The effect of these organisms' heading vectors on the resulting track vectors is virtually insignificant, but what distinguishes them from inactive particles is that they also have a capability for propulsive ascent [27–29]. They can thus strongly influence their movement trajectories by selecting swimming depths or flight altitudes to coincide with favourable currents. Active selection of swimming depth, for example, has been shown to produce profound differences in the drift trajectories of organisms such as jellyfish, flatworms, copepods and larval fish [16,28–32]. Weak-flying insects, such as aphids, can determine when they take off and exert some control over their height within the air column when migrating and also over when they land. Their airborne movements are thus not entirely passive [27] and are quite distinct from those of plant seeds and wingless arthropods which are completely at the mercy of the wind once they have launched [22].

Finally, the movement of relatively fast-moving organisms can, under special circumstances, approximate passive downstream transport if the heading vectors (speed and direction relative to the surrounding medium; Figure 1) have no net velocity. This may occur via one of two mechanisms: at the individual level (because the individual displays erratic headings that are approximately random over time),

Box 1

Vector addition and constraints on movement in preferred directions.

The rate at which an organism's movement occurs is a vector quantity, the *velocity*, which incorporates both speed and direction. The organism's *track vector* (which expresses its speed and direction relative to the ground) is the sum of its *heading vector* (its speed and direction relative to the surrounding fluid) and the *flow vector* (the direction and speed of the wind or current) [40]. This sum can be represented by a *triangle of velocities* (Figure 1) in which the lengths of the sides represent speeds and the angles at which they are drawn represent directions.

An animal that can move itself through a medium (air, water) that is flowing will have some degree of influence over its track direction and ground speed. Assuming the animal propels itself at some fixed 'cruising speed', its only means of influencing its track vector will be by changing its heading. However, the animal will only be capable of achieving the full 360° range of possible track directions if its locomotory speed exceeds that of the flow. If this is not the case, the range of possible track directions is restricted to a sector $\pm\beta°$ from the downstream direction (Figure 2), where β = arcsine (a) and a is the ratio of the animal's speed to the speed of the flow [88].

Animals that can usually out-fly or out-swim the flows in which they move include migrating birds (with sustained airspeeds of 8–23 ms^{-1} [98]) and large fish and adult sea turtles (sustained swimming speeds of 1–3 m s^{-1} [95,97]); in contrast, insects, larval fish and hatchling sea turtles are relatively slow-moving and their range of potential track directions will very often be severely restricted (Figure 2). However, even fast-moving animals will quite frequently encounter flow speeds that significantly affect journey times and energy expenditures, or that will drift them significantly off their preferred course. Examples of how both slow-moving and fast-moving animals respond to flows are described in the main text of this review.

or at the population level, because each individual takes up and sustains a particular heading, but these are distributed randomly over 360°. For instance, in the brown planthopper (*Nilaparvata lugens*), migrating individuals have been observed to orientate in all possible directions [33] — though which of the two mechanisms this arises from is unknown. Also, individual adult leatherback turtles (*Dermochelys coriacea*) show random orientation with respect to current directions during their transoceanic migrations (P. Luschi *et al.*, unpublished data), and thus some very large organisms may effectively adopt this strategy too. Disorientation of migrant birds in overcast cloud, heavy rain or thick fog produces a similar effect, though birds generally avoid migrating in such conditions [34].

Active Downstream Orientation

This strategy involves the organism taking up a heading coincident with the downstream direction (Figure 3B), thus maximizing its displacement speed and travel distance in a given time. This strategy can be expected to evolve whenever rapid displacement speed and short journey duration are more important than precise travel direction and the ability to reach a highly-localized goal. An essential component of this strategy is an ability to detect the flow direction once the animal has launched into the flow, and to orientate accordingly.

Active downstream orientation is often considered the norm among large nocturnal insect migrants flying hundreds of meters above the ground — radar entomology studies have frequently demonstrated that these species take up a common orientation, usually close to the downwind direction [6,35,36]. The great majority of windborne long-range insect migrants do not have to reach a localized goal; but due to the brief physiological 'windows' during which migration is possible in many species, speed is of the essence. Active downstream orientation would thus seemingly be adaptive because large migrating insects would add their not inconsequential self-propelled airspeeds (2–6 m s^{-1}) to the wind, and thus significantly increase their migration distance [9,37,38]. However, this requires the insects to 'sense' the wind direction and maintain their downstream orientation while flying hundreds of meters above the ground and often under conditions of severely reduced illumination (Box 2).

Downstream orientation is the most adaptive behaviour in some semi-arid and desert environments, because insects employing downwind movement will be carried towards 'wind convergence zones', thus increasing their chance of reaching areas where rainfall is likely [39]. Escape flights by migrant birds that experience difficulties over the sea or desert [40] provide a second example. In other circumstances, however, active downstream orientation appears to be little used by birds, despite their frequent selection of reasonably favourable tailwinds for departure [11,41,42].

Active downstream orientation is thought to be rare in marine species because it is difficult for pelagic organisms to assess the direction of oceanic currents; no mechanism for directly detecting the flow in the absence of stationary reference points is widely accepted [19,20,43]. However, the strategy of 'selective tidal stream transport' exhibited by continental-shelf fish such as plaice (*Pleuronectes platessa*) [44] and cod (*Gadus morhua*) [45], and invertebrates such as the blue crab (*Callinectes sapidus*) [46], indicates that certain species are capable of sensing the direction of a tidal flow. Migrating plaice move into mid-water to take advantage of the tidal current when it is favourably directed, and in addition they maintain orientation in the downstream direction (even at night when visual cues to facilitate this are not available) so that they increase their movement speed. Then when the tide turns they descend to the seabed and wait until the favourably-directed flow returns [44]. The mechanism for detecting the tidal stream direction is unknown [44], but the benefits of this strategy are clear: the metabolic cost of transport is about 20% lower than continuous mid-water swimming [47]; it results in rapid long-distance transport [48]; and migration occurs along consistent geographical routes, resulting in a high degree of spawning-area fidelity [49]. Selective tidal stream transport is also exploited during long-distance river-travel events by estuarine crocodiles (*Crocodylus porosus*), which swim in surface water currents when these are favourably directed but dive to the river bed or climb out onto the bank when
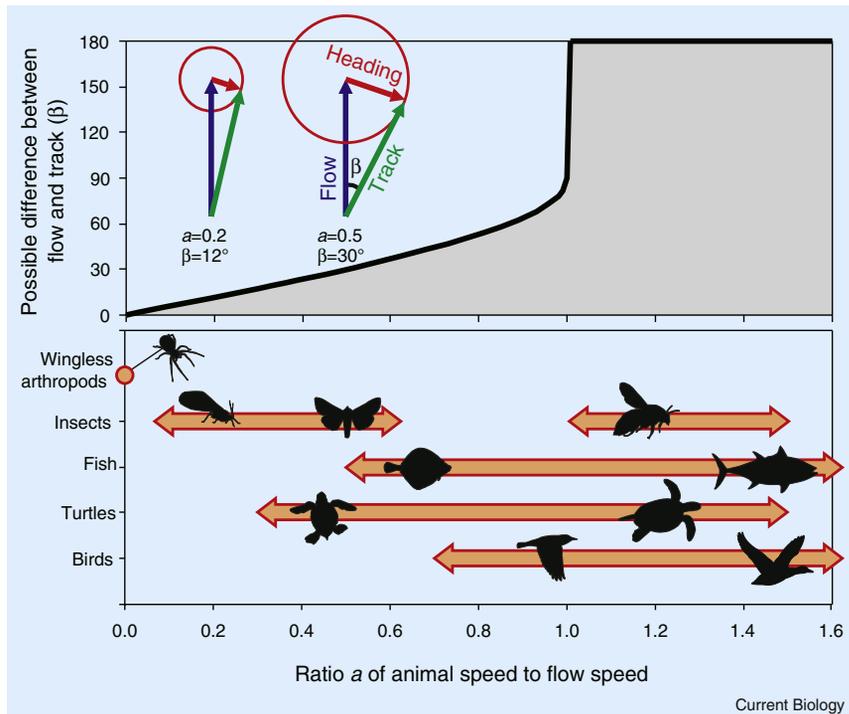
Figure 2. Effect of animal speed and flow speed on movement track.

Top panel: The relationship between the direction of resultant movement track in relation to the flow direction (β), and the ratio of the individual animal's speed to the flow speed (*a*). The grey field shows possible angles of movement in relation to the flow direction and the thick line shows the maximum possible difference between track and flow direction (±β°, see insets for two examples). Bottom panel: Examples of species in the major taxonomic lineages discussed, showing typical values of the speed ratio (*a*). Typical wind speeds were assumed to be 2–16 m s^{-1} [14], and typical ocean currents were assumed to be 0.25–2.5 m s^{-1} [93]. Typical sustained flying or swimming speeds were assumed to be as follows: top row: ballooning spiders (0 m s^{-1} [23]); second row: aphid (0.5 m s^{-1} [94]), a noctuid moth (4 m s^{-1} [14]), and a bumblebee (7 m s^{-1} [68]); third row: a slow-moving flatfish (0.35 m s^{-1} [47]) and a fast-swimming tuna (3 m s^{-1} [95]); fourth row: a hatchling (0.3 m s^{-1} [96]) and adult (1.5 m s^{-1} [97]) pelagic turtle; bottom row: a nocturnal passerine migrant (10 m s^{-1} [98]) and a day-migrating duck (25 m s^{-1} [98]).

they are contrary [50]. Crocodiles are incapable of prolonged bouts of sustained swimming [51], and so their long-range movements on tidal river currents presumably involve both active downstream orientation and passive downstream transport — which would make *C. porosus* (the world's largest living reptile) the biggest passively-drifting animal.

We also regard the oceanic movements of hatchling loggerhead turtles as a form of active downstream orientation. It is generally assumed that hatchling turtles, because of their limited swimming abilities and positive buoyancy, are passively drifted by ocean surface currents during the first few years of their life [10,52]. However, laboratory experiments have indicated that loggerhead hatchlings take up swimming directions in response to geomagnetic cues within and beyond parts of their natural range (the North Atlantic gyre) that would tend to align their heading with the local current direction [53–55]. It has been suggested that this may help to keep hatchlings within the large-scale flow and facilitate their movement along the migratory pathway [53]. Recent satellite-tracking experiments with displaced loggerhead adults indicate that they probably identify the downstream direction [56]. Likewise, in northern fur seals (*Callorhinus ursinus*), migratory routes to productive winter feeding regions appear to exploit favourably-directed ocean surface currents [57], which also suggests a similar capacity. However, in both cases precise data on the animals' headings and surface current directions are required to confirm that these species do engage in active downstream orientation.

### Compass-Biased Downstream Orientation

In compass-biased downstream orientation an organism deviates its heading slightly from the downstream direction, so that it lies between the downstream and the goal direction (Figure 3C). The net result is that the movement track will be closer to the goal direction than it would have been if the

animal moved perfectly downstream, but not as close as if it persistently headed towards the goal irrespective of the flow direction (full drift). However, fast travel speeds are achieved because a large component of the organism's self-propelled speed is directed downstream. Thus, compass-biased downstream orientation can be seen as a trade-off between moving fast and moving in the preferred direction.

Organisms that are dependent on transport in fast-moving flows, such as insects that can only migrate for just a few days, will have limited opportunities for movement in the seasonally-favourable direction if winds blowing approximately in this direction are scarce. If such species are migrating towards an extensive geographical region rather than a highly-localised goal, or if they have to cross a region of very unfavourable habitat so that distance covered is more important than a precise track direction, compass-biased downstream orientation may provide the best chance of a successful migratory outcome. Recently it has been shown that large, high-flying migratory moths offset their headings by a small degree when the downwind direction veers more than 20° away from the seasonally-preferred direction [37,38], resulting in comparatively fast movements that are 20° closer to the preferred direction than would have been achieved by flying downwind [9]. In fact, ground speeds and flight directions of nocturnally-migrating noctuid moths and passerine birds are surprisingly similar [14]. Compass-biased downstream orientation has not been widely reported but could be characteristic of species that migrate seasonally towards broad geographical areas, especially if they have slow self-propelled speeds (in relation to the flows in which they travel) and short migration windows.

Full Drift (Constant Compass Orientation)

Full drift is a strategy for maintaining a constant compass heading towards the goal direction, regardless of the flow
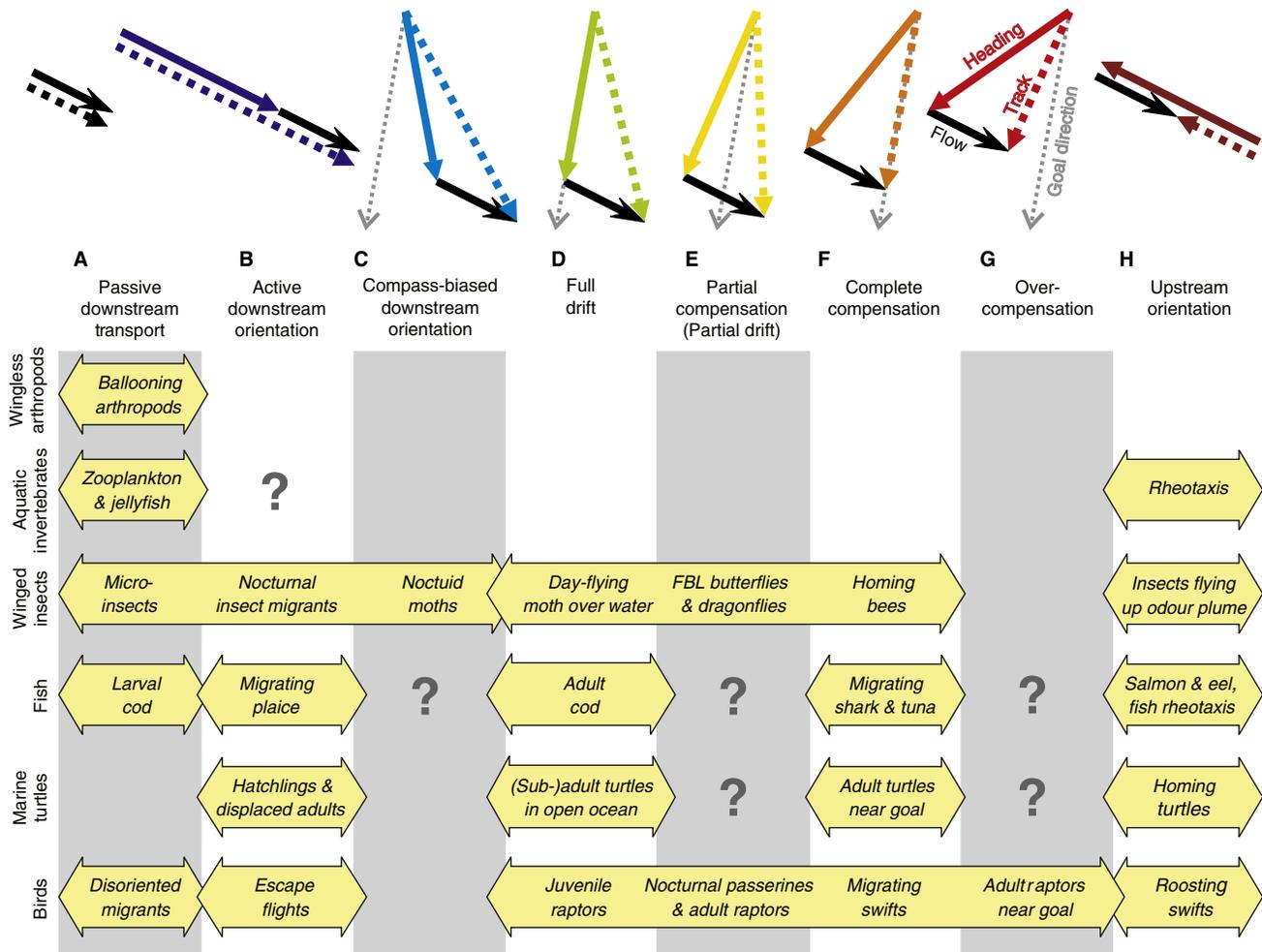
Figure 3. The eight possible orientation responses to flow.

Top panel: Triangles of velocities for the eight possible orientation responses (A–H) that a swimming or flying animal can take up with respect to the flow direction. Each diagram shows the flow vector (solid black line), the heading vector (solid coloured line, not present in A), the resultant track vector (dashed coloured line), and the preferred goal direction for those strategies which imply the animal has one (dotted grey line, C–G only). Bottom panel: Examples of the different orientation strategies that have been observed in the major animal groups discussed. Where arrows span several categories, this indicates that a continuum of responses may be found in a broadly similar group of animals. The three groupings here are: nocturnal, high-flying windborne migrant insects (A–C); low-flying diurnal insects within their flight boundary layer [87] (D–F); and typical nocturnal and diurnal bird migrants (D–G). The figure demonstrates that many of the major taxonomic groups display most of the strategies, but that we apparently know least about the orientation responses of fish.

direction (Figure 3D). An organism will therefore drift fully whenever the flow is not coincident with the intended track. If the flow is consistent, a large lateral displacement may accumulate. Full drift may arise either through the organism being incapable of assessing the flow direction or because it takes no action to compensate for it. The latter situation is presumed to represent an evolved response to particular flow conditions, and is sometimes termed 'adaptive drift' [12].

Assessment of the flow direction is difficult in the open ocean, and thus full drift is probably common in swimming oceanic migrants [19,43]. For example, migrating cod are drifted successively to the left and then to the right by successive tides, while maintaining a constant compass heading across the tidal stream axis [45]. Observed movement trajectories of the most intensively-studied group of

pelagic migrants, the sea turtles, clearly demonstrate that oceanic currents exert a dramatic influence on their pathways [10,43,58–61]. Recent high resolution GPS tracking is starting to reveal that marine turtles do not follow straight-line routes during oceanic crossings [62,63], which indicates that they swim on a constant compass bearing and are drifted by currents.

By contrast, flying animals will often be capable of assessing the flow direction during flight, particularly day-flying species travelling over solid terrain, and thus permitting full drift under such conditions probably constitutes an adaptive response. There are some occasions where flying animals seem incapable of assessing the wind direction — nocturnal passerines migrating at high altitudes [5,40], for example, or diurnally-migrating *Urania* moths flying over water [64] — but it is quite possible that in these studies the species

Mechanisms for sensing flow direction.

Travelling animals must be able to determine their position relative to the target location (the 'map step') and be able to maintain their heading along the direction required to reach the goal (the 'compass step') [1,4,18,19]. Animals that use only their biological compasses will be subject to full drift; all other types of drift or compensation require that the animals can directly or indirectly sense the flow of the medium.

Direct flow sensing
Direct assessment of flow direction is a challenging task for swimming or flying animals, as it is generally assumed that proprioceptive information related to flow direction is not available. However, features of wind turbulence may allow high-altitude nocturnal insect migrants to determine the downwind direction [35,36]. The sensory mechanism for detecting these weak turbulent flows remains to be elucidated, but the antennae may play a role [99]. Turbulence may possibly also be used by birds and bats to sense wind direction, as suggested by the recent identification of extremely sensitive wind-detecting hairs on bat wings [100].

Indirect flow sensing
Animals may also indirectly detect the effects of flow if they use a map sense based on topographical features and landmarks. Depending on the sensory mechanisms the responses to the flow may be immediate or delayed. Some taxa gather information about flow direction by assessing the effect of flows on their movement path. Migrating birds, for example, visually assess their movement direction relative to features of the terrain, or wave patterns below [40,67]. They can then adjust their headings appropriately to mitigate drift. Similarly, some day-flying insects also use ground features to assess wind direction, and may also use stationary landmarks to compensate for drift [64]. Given nocturnal insects' high sensitivity to optic flow [101], there may also be a role for visual assessment of movement relative to the ground at night, especially under conditions of higher (moonlight) illumination. Similar visual mechanisms are not available to open sea migrants, and marine organisms are thought to be generally unable to directly detect ocean current directions [19]. Thus, most pelagic migrants will only be capable of sensing current drift once they have been displaced considerably from their preferred track, by relating their current geographic position to the position of their goal. In some cases, the Earth's geomagnetic field probably serves as the source of 'map' information [102], including in spiny lobsters (*Panulirus argus*) [103], loggerhead turtles (*Caretta caretta*) [53,54] and green turtles (*Chelonia mydas*) [78].

concerned were capable of detecting the flow, but chose not to compensate for drift as it was more adaptive to delay the compensation until nearer the goal. Indeed, full drift appears to be optimal in three situations: first, when there is a balance between crosswinds from the left and right along the route, as is the case for birds migrating from North to South America across the western Atlantic Ocean, where prevailing winds will firstly drift the birds towards the east and then the west [65]; second, juvenile birds, on their first (autumn) migration, if unaccompanied by adults, often travel on an inherent compass bearing, and full drift will be adaptive because the precise goal location is only learned after the first migration has been completed [66]; third, when far from the goal, it is optimal to defer compensation as drift in the opposite direction may be encountered later [21]. Such flexibility, with full drift largely limited to the early stages of migration, was recently demonstrated for adult raptors [15].

Partial Compensation
Partial compensation (or partial drift), involves the organism shifting its heading from the goal direction towards the upstream direction (Figure 3E), so that the resultant track is closer to the goal direction than with full drift but not enough to completely compensate for the effect of flow. Partial compensation appears to be the most frequent response to lateral wind drift during goal-directed movements in flying animals. The majority of studies of migrating birds have reported some degree of compensation for wind drift, although the relative amount of drift and compensation shows considerable variation [5,15,40]. Cases with a relatively small element of drift and a large element of compensation include adult raptors tracked by satellite [66], while wind

drift is much more significant during high-altitude shorebird migration over the Arctic [12]. Birds probably sense the flow by visual assessment of ground features, which may explain why high-altitude and nocturnal migrants [5], as well as birds migrating above the sea [67], tend to show lower levels of compensation than low-altitude, diurnal migrants [15,66].

Partial compensation is also commonly observed in low-flying migratory butterflies and dragonflies, even when flying over water [64]. These insects fly just a few meters above the surface and, like birds, presumably use optic flow to gauge their speed and degree of drift. These field observations of naturally-migrating birds and insects indicate that they are not constrained to move solely along a fixed compass bearing, but can sense the flow direction and change their heading in an adaptive manner. Through partial compensation flying animals thus exert a high degree of spatio-temporal control over their movements. By contrast, on current evidence, most marine fish, reptiles and mammals don't appear to employ partial compensation [43,45,50, 57,58], although the higher resolution tracks of pelagic migrants and the better estimates of ambient flows now becoming available will allow this picture to be tested more rigorously.

Complete Compensation
This strategy involves an animal altering its heading into the flow to such an extent that it achieves a track coincident with the goal direction, irrespective of the flow vector (Figure 3F). It is the theoretically optimal behaviour for animals navigating towards a precise goal when the direction of the flow is constant throughout the journey [21]. Complete

compensation requires a precise mechanism for detecting flow direction, or the ability to accurately measure its effect on the track direction relative to the substrate, and for the animal to respond accordingly (Box 2).

The best-documented examples of complete compensation are found in short non-migratory movements, when the flow direction is likely to remain constant and accuracy is paramount. For example, homing worker honeybees (*Apis mellifera*) and bumblebees (*Bombus terrestris*) maintain a 'beeline' (i.e. a virtually straight path) between a forage patch and their hive even in strong crosswinds [68,69]. A homing bee has the advantage of being able to continuously assess her compensatory performance, and by adjusting her heading until the ground image movement over the retina occurs at the angle relative to the sun's azimuth corresponding to her intended track, she is able to continuously correct for errors [68]. This is not the case for the fruit-catching fish *Brycon guatemalensis*, which makes a decision about the heading required to compensate for drift before it begins to swim [13]. Shoals wait under ripe fruit trees and when they see a fruit falling they immediately swim along a heading that accounts for the prevailing current direction, so that it will take them directly to where the fruit will hit the surface. By swimming the straight line (i.e. compensating completely for the flow) the fish decrease the time required to reach the fruit by up to 10% [13]. This might be decisive as competition for falling fruits is strong.

As predicted by theory [21], animals that make long migrations do not seem to engage in complete compensation persistently throughout the journey. Although there are apparent examples among the transoceanic migrations of sharks and tuna [70,71], the spatial and temporal resolution of these tracks is too poor to elucidate the exact relationship between the fishes' headings and flow directions. For long-distance migrants, complete compensation seems rather to be part of a strategy in which the orientation response to the flow is adjusted to the local environmental context. Indeed, many animals compensate during parts of their journeys. For example, blue sharks (*Prionace glauca*) can maintain a consistent track in the open sea for hours or even days [72], and humpback whales (*Megaptera novaeangliae*) apparently show complete compensation for lateral current drift during several days of continuous movement extending over 200 km in length [73]. Some cases of complete compensation are also known for birds passing a specific region or site, mainly birds flying over land during the day [67] and at very low altitude during the night [74], but also in migrating swifts (*Apus apus*) [75]. For animals that generally allow a degree of drift during their travels, complete compensation may be particularly important during the final approach as theoretically predicted [21] and recently documented for migrating raptors [15]. Annual, long-distance return movements between known feeding and spawning grounds are also a common aspect of the life histories of many migratory fish [76,77], turtles [43], and marine mammals [73], indicating a well-developed capacity to compensate for drift at some point during their migrations. Determining their position in relation to their goal during these final stages of migration may involve geomagnetic cues and perhaps also wind-borne cues [54,60,78,79].

Overcompensation
During overcompensation, the animal alters its heading with respect to the flow to such an extent that its track direction is shifted beyond the goal direction (Figure 3G). Overcompensation rarely occurs in isolation; it is usually preceded by occasions where the animal has been drifted off course, and thus is a delayed correction for previously-sustained drift [15]. This orientation response is best known from diurnal bird migrants flying at low altitudes; it has been suggested that these low-altitude overcompensation flights are part of a strategy whereby diurnal migrants combine high-altitude flights involving partial drift with overcompensation on a subsequent leg [80].

Upstream Orientation
This strategy involves the animal maintaining its heading directly into the flow (Figure 3H). Upstream movement is commonly observed during foraging and mate-searching movements [81], when both flying and swimming animals make use of bilateral sensory perception of current-borne chemicals to track odour plumes upstream to their source [82,83]. Persistent upstream orientation for the purpose of maintaining a position within a flow, known as rheotaxis [84], is common among fishes, amphibians and aquatic invertebrates. It helps to reduce passive drift while maximizing perception of chemical cues and interception of prey. Analogous to rheotaxis is the curious nocturnal roosting-flight behaviour of swifts, which spend the night aloft (possibly sleeping on the wing) and orient upwind, presumably to maintain themselves within, or at least close to, their home-range [85].

By comparison, persistent upstream orientation is a relatively uncommon strategy in long-distance migration, because the energetic costs of sustained movement into the flow are prohibitively high. Spectacular upstream movements do occur, however, during the final stages of the migration of salmon [86] and eels [31], which leave the ocean and travel great distances upriver against the current. Similarly, migrating butterflies and dragonflies flying close to the substrate within their 'flight boundary layer' [87] can make progress against headwinds, and so will on occasion carry out persistent upstream movements. Also birds, not least diurnal migrants like low-flying finches and starlings, regularly fly into more or less opposed winds, but this probably does not reflect headwind orientation *per se* but rather a large tolerance for migrating under variable wind conditions [14,88].

It should be noted that animals heading consistently towards their goal while being subjected to drift by a rather constant cross-flow during the migratory journey will often end up on the downstream side of the goal and will thus have to move upstream during the final approach phase to the goal [21]. Hence, one should expect that upstream movements are particularly frequent near the animals' final destinations (see complete compensation). A peculiar example of upstream orientation during a long-range migration is provided by green turtles homing to Ascension Island in the Atlantic Ocean from feeding grounds off the Brazilian coast. Artificially displaced turtles were far quicker to relocate their nesting beaches when they were released downwind of the island than upwind of it [79], indicating that windborne cues (olfactory and/or auditory information) emanating from the island are used to relocate it. This case of course differs from all those previously considered in that the ambient flow the turtles are responding to is not the same as the medium through which they are propelling themselves.

Conclusions

Animals show highly flexible and complex orientation responses to flows. A striking feature is that a wide variety of orientation responses are present in many of the major animal groups (Figure 3). We thus conclude that distantly-related organisms show a great deal of convergence in the ways in which they solve the common problems of utilizing available transport in the form of favourable flows, and of coping with contrary flows. Individuals may adopt different responses to flows during distinct movement stages, perhaps taking advantage of different flow directions and speeds at discrete depths or heights.

Analysing the variations in directions between samples of migrants passing a certain site under different flow conditions has produced most of the current knowledge about drift responses by birds and insects, but this approach is sensitive to potential biases and responses to events during prior stages of the migration. This highlights the importance of tracking the entire migratory routes of individuals so that drift behaviour can be analyzed along the entire movement pathway. Such approaches are a particularly difficult challenge for the smallest migrants.

Our review also illustrates that birds and insects have been studied much more intensively than marine animals. In fact, surprisingly little is known about how marine animals respond to currents, aside from the well-known case of selective tidal-stream transport. Disentangling the role of passive drift versus active swimming is complicated with marine species, as estimates of current speed and direction at precise locations and times have limited accuracy. Currents at the location of tracked animals have been estimated from ocean dynamic models and from satellite measurements [59], but both methods have limitations [89]. Thus, it is clear that there is still much to learn about the current-detection capabilities of ocean-dwelling animals, and more accurate movement tracks combined with simultaneous data on current speeds and directions are required for making progress.

While much of the variability in the responses of animals to flows can be attributed to adaptive strategies for exploiting transport and dealing with drift, some variation will be due to the animals' inability to detect the flow or to the limited precision of their estimates of its direction and speed. A major challenge for the future is to distinguish between adaptations and sensory limitations in the different types of orientation response. Cross-disciplinary approaches, involving ecologists, sensory biologists, mathematical modellers, fluid physicists and engineers [90,91], and exploiting new technologies [6,8] as well as traditional methods, will be imperative. Comparative studies of multiple taxa moving under natural conditions will be indispensible in the search for general rules describing how distantly-related animals sense and respond to flows [14,92]. We hope this review will help inspire such collaborative endeavours.

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