Wind and orientation of migrating birds: A review

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Summary. Migratory flights are strongly affected by wind, and birds have developed many adaptations to cope with wind effects. By day, overland migrants at high altitudes may often allow crosswinds to drift their tracks laterally from the preferred heading. In contrast, many birds at low altitude adjust their headings to compensate for drift, and may overcompensate to allow for previous drift. The relative motion of landscape features is probably used to sense drift, at least by day. By night, some overland migrants compensate fully for drift but others do not; no pattern is obvious. Over the sea, compensation is rarely if ever total; wave patterns may allow partial compensation. Other adaptations can include reduction of drift by flying at times and/or altitudes without strong crosswinds. Some birds recognize the need to change course to allow for previous wind displacement, and reorient at least roughly toward the original route or destination. Some juveniles en route to previously-unvisited wintering grounds seem to have this ability, but corroboration is needed. Such reorientation may not require a true navigation ability. However, some birds have unexplained abilities to sense the wind while aloft.

Key words. Bird migration; orientation; wind; drift; pseudodrift; compensation; reorientation; vagrancy; landmarks; leading line; soaring.

Introduction

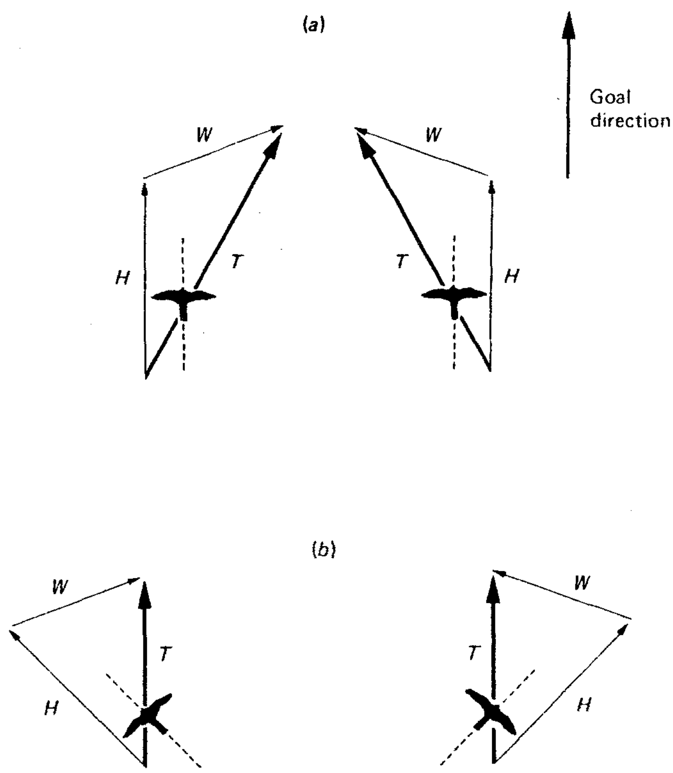
The *track* of a bird over the ground is the vector sum of its direction and speed through the air (*heading*) plus the wind direction and speed (fig.). Wind speed is often a significant percentage of the bird's airspeed, especially for small slow-flying species and for soaring birds. Thus, variations in wind can have major effects on the energy cost of flight and on orientation.

Birds can cover a given distance quicker and at less energy cost with a tailwind than with a headwind. If headwind speed exceeds a bird's airspeed, it may even be blown backward in *retrograde migration*[2, 58, 93]. Presumably because of this, there tends to be more migration on occasions with more or less following winds[121, 127]. However, following winds are rare along some important migration routes[68, 119], so some birds must migrate with cross or opposing winds. Also, even when birds take off with following winds, those winds may not persist throughout the flight. Furthermore, minimization of the energetic cost of flight is not the only selection pressure acting on migrants, and it may be advantageous for certain birds not to fly with following winds[11, 115].

Flight with crosswinds causes orientational complications; the bird's track is not the same as its heading. If the bird continues to head in its *preferred* or *standard* direction, it will travel in a direction somewhat different from the preferred one. However, it might instead *compensate* by adjusting its heading so that its track is in the preferred direction (fig.). Partial compensation is also a possibility. In extreme cases, strong winds, often combined with other conditions that hinder orientation, sometimes displace migrants far outside their normal range.

If compensation occurs, how does the bird recognize that its track is being *drifted* laterally from the preferred heading? Under what conditions can birds sense wind direction and speed while aloft? Conversely, if real-time compensation is lacking or only partial, then the bird's track and landing point will be partly a function of unpredictable wind conditions. In this case, can birds somehow compensate during later flights?

Wind itself may sometimes be used as a directional cue, most likely to maintain a bearing selected using other



A bird's track velocity T (speed and direction relative to ground) is the vector sum of its heading velocity H (speed and direction relative to air) and wind velocity W. *(a)* Birds flying on a constant heading will be drifted by winds with a cross component. *(b)* To maintain a constant track direction in varying winds, birds must adjust their headings into the wind. From Alerstam[15].

cues[134], but possibly even as a primary cue[47]. A few workers have reported that some migrants orient downwind when visibility is poor[6, 7, 142] and perhaps under clear skies as well[1]. If so, how do birds sense wind direction while aloft, especially with poor visibility?

Methodology

This review is based almost entirely on field studies of migration in progress. No useful procedure has been developed to allow direct tests of wind effects on orientation of captive migrants. However, cage studies have been useful in evaluating whether migrants can reorient to compensate for earlier wind displacement[3, 52, 113, 114].
Almost all relevant field studies have been observational, and in the absence of experimental control have encountered the usual difficulties in distinguishing causal and coincidental relationships. This problem is compounded by three facts: 1) Even when the species is known (which is usually not the case in radar studies), the specific origis, destination, and preferred track of a passing migrant are almost always unknown. Without this information, it is uncertain whether the bird is compensating for lateral wind drift from a preferred heading. 2) Relationships between orientation and wind are expected to be quite variable, depending on type of bird, stage of the migration, flight altitude, whether it is day or night, and whether the bird is over land or sea[13, 14, 18, 19]. 3) Migrants may respond to a variety of directional cues, and a simple analysis of behaviour in relation to one cue may reveal little about its importance[47, 48].
Despite these problems, much useful information about wind effects on orientation has been obtained by visual and surveillance radar studies of migration, including many studies done 15–40 years ago (reviewed by van Dobben[43], Lack[83, 86, 88], Gruys-Casimir[65], Evans[53], Emlen[47], Alerstam[9]). These 'traditional' methods can still provide important new data[67, 68, 71, 124]. However, a few studies using special methods have been of particular value. *Tracking radar* has provided detailed data on behaviour of individual birds migrating at measured altitudes, sometimes in well-defined conditions of wind and visibility. The few studies in which migrants have been *released aloft* and subsequently tracked by radar[7, 46, 49] provide the only data on orientation of free-flying migrants subject to experimental control. *Radio-telemetry* allows tracks and headings of known individual birds to be determined throughout a flight, and sometimes during several successive flights with varying winds and other cues[28, 39, 40, 138]. *Simultaneous observations at different sites* can also be valuable[30, 96, 140]. Further use of these special methods will be important in resolving uncertainties about wind vs orientation.

Detection of wind while aloft

The presence of lateral drift by crosswinds is obvious to a pilot if he can see two or more specific points on the ground along the desired heading. These points do not need to be previously known features. If the features do not remain aligned and directly ahead as the flight progresses, there is lateral wind drift. To compensate, the heading of the aircraft is adjusted until ground points along the desired course remain aligned. A related method is to fly on the desired heading and observe, directly or with a drift meter, the apparent motion of landmarks directly below. If their motion is at an angle to the heading, the heading is adjusted correspondingly. However, when flying in or above clouds, or at night over a landscape lacking discernible features, pilots without modern instruments cannot sense lateral drift. Even when visibility is good, drift is harder to detect at higher altitude because of the slower apparent motion of visible reference points.
Many birds flying overland during the day can correct for lateral drift, presumably using landscape features as do pilots[35, 43, 65, 132]. Some authors have denied that this process occurs at night. However, there probably are sufficient landscape cues at many places and times, especially with moonlight[24]. In addition, man's lights now provide suitable artificial beacons in many regions. However, only the most conspicuous natural features (coasts, major ridges) are visible on moonless or overcast nights[24], so visual detection of drift may be impossible then. Bingman et al.[30] found evidence of drift compensation only by nocturnal passerine migrants flying near a large river, suggesting that birds did not use the artificial lights in nearby regions away from the river.
Fixed landmarks are not available in the open sea, and lateral wind drift is apparently more common there than overland[9] (see below). This is consistent with the idea that landscape features are important in recognizing and compensating for wind drift. However, waves might be useful in judging drift, either as reference points or because their orientation is related to wind direction[41, 60, 83]. Three species migrating overwater during daytime compensated incompletely for drift[18]. They seemed to attempt to compensate using waves as landscape features, without allowance for the fact that waves move in a way related to the wind, but at reduced speed.
Several lines of evidence indicate that some migrants, while aloft, can sense the wind without viewing the landscape. 1) Certain birds apparently select flight altitudes where winds are most favourable[15, 16, 40, 119, 131], possibly even when above clouds[33]. 2) Griffin[61] found evidence of partial compensation for lateral wind drift by birds flying within cloud at night. 3) Able found that landbirds flying at night tended to fly downwind when celestial cues were hidden by cloud[6] or when form vision was blocked by frosted contact lenses[7]. 4) As expected on energetic grounds[107], airspeeds of nocturnal migrants are negatively related to the tailwind component, suggesting that they sense the wind and adjust their flying effort accordingly. This has been confirmed for various

groups of migrants[31], within particular species[46, 138], and for single birds[2]. This effect has also been found over the sea, indicating that view of a stationary landscape is not necessary to detect the wind[92].

This evidence shows that some birds can sense wind direction, at least crudely, without visual contact with the ground. It is not known how general this ability may be, nor what the mechanism is. However, two possibilities have been suggested. 1) Griffin[60, 62, 64] suggested that localizable noise sources on the surface could be useful in detecting wind drift without visual cues. Flight calls of the migrants might also be used in some way[4, 60]. 2) Nisbet[102] suggested that birds sense wind direction and speed based on anisotropic patterns of air turbulence, which are related to wind direction. The pattern of accelerations experienced by a bird flying in turbulence may depend on the angle between the flight and wind directions. Although both hypotheses seem plausible, there is little evidence for either.

The turbulence hypothesis is often discussed[4, 23, 24, 47, 60, 63, 96], but the evidence is meagre: a) Vleugel[133, 135, 136] suggested that few birds migrate in calm periods, and that the absence of directional wind cues was the reason. However, his data on numbers aloft were subject to detection biases. b) Tracks of migrants flying below or in cloud, when knowledge of wind might be especially important, are sometimes less straight than normal[5, 49, 61]; slight changes in heading might be important in sensing turbulence[49]. c) There is limited evidence that nocturnal passerine migrants tend to concentrate at times and altitudes where the air is unstable and turbulent[24, 96], although Kerlinger and Moore[79] suggest that migrants may tend to avoid turbulent air for other reasons.

In summary, many diurnal migrants clearly sense and allow for the effects of wind on their tracks, probably by reference to the landscape. This mechanism probably is used to a lesser extent at night. At least by day, some migrants over the sea appear to sense and partially correct for the wind, possibly based on wave patterns. In some situations, migrants seem able to sense wind direction without seeing the surface, perhaps by detecting 'acoustic landmarks' or turbulence patterns related to wind direction. Methods of wind detection at night, over the sea, and in poor visibility all need more study.

Concepts of lateral wind drift and compensation

Optimum strategies

One might think that each bird should compensate continuously for lateral drift so as to fly along a straight line between its summer and winter grounds. This would be the shortest possible route and would avoid the need for an ability to reorient toward the route or the destination after lateral displacement. However, this strategy is not necessarily practical or desirable even if the bird can compensate for drift. Alerstam[13–15, 19] has shown, following earlier suggestions by Rabøl[109, 111], that some birds would require less time or energy to complete their migrations if they tolerate uncorrected wind drift during parts of the migration and compensate at other times. However, this would require an ability to detect and correct for previous displacement from the straight-line route. It is not clear how many birds have this ability, especially in the case of juveniles en route to the wintering grounds for the first time[4, 47, 108].

Alerstam's models indicate that compensation for drift is advantageous if winds blow from a constant direction throughout the migration, as may occur for some short-distance migrants. However, if winds vary along a lengthy migration route, and if there are no specific obligatory stopover points en route, flying time and energy costs can be reduced by allowing lateral drift during early flights, and then by compensating when nearing the destination[14]. Migrants may also save time and energy by tolerating drift early in a flight while taking advantage of strong partly-following winds at high altitude, and then correcting for the drift by a partly-upwind flight at lower altitude where winds tend to be weaker[13]. Several studies have provided evidence consistent with some of Alerstam's predictions, as summarized later.

Pseudodrift

Until 1966, it was assumed that correlations between crosswind and mean track were evidence of at least partial wind drift. However, Evans[50] and Nisbet and Drury[103] noted that this correlation would be expected even if all birds compensate for lateral wind drift, since many birds tend to fly on occasions with more or less following winds relative to their own individual preferred headings[121, 127]. This selectivity seems to exist not only for the multi-species groups usually studied by radar, but also within some species, viz. eider[17], wood pigeon[21] and (less convincingly) lapwing[88] and starling[67].

Pseudodrift is a major complication when interpreting field data on flight orientation. Reanalyses of data initially assumed to show lateral wind drift suggested that most overland cases and some offshore cases might instead be pseudodrift[9, 88, 103]. However, suggestions that true drift is rare overland[9] were premature[14]. In the absence of data on destinations of passing migrants, it is rarely possible to determine whether correlations between track and crosswind are solely attributable to pseudodrift. Uncorrected drift is now expected in some situations[13, 14]. In some studies, pseudodrift is an unlikely explanation for the track-crosswind correlation because the apparent drift effect seems too large[9, 12, 124] or for other reasons[68, 71].

The difficulty in separating pseudo- from actual drift persists today. This is especially true when species are indistinguishable, as during radar and nighttime visual studies. When tracks are unrelated to wind, one can be confident that there is compensation for drift. However, in the common situation when tracks are correlated with wind, it is usually uncertain whether pseudodrift, true drift or both are involved.

Telemetry studies that provide data on known species flying in varying winds provide a way to overcome this problem. Cochran's telemetry data from thrushes flying inland at night[39,40] showed that headings were not adjusted to compensate for wind drift. However, thrushes tended to select flight altitudes where drift was minimized. With this strategy, net tracks of thrushes followed for two nights ($n = 3$) or six nights ($n = 1$) were similar to preferred headings even without active drift compensation[39,40]. This is consistent with the idea[13-15] that it may be counterproductive to expend extra energy compensating actively for lateral drift when far from the destination.

Although pseudodrift complicates analysis of flight behaviour, the existence of this phenomenon is itself an indication of the close attunement of birds to wind. Pseudodrift occurs because birds with different preferred tracks, e.g., SSE vs SW, tend to migrate with following winds relative to their own tracks[42,121,127].

Evidence of lateral wind drift and compensation

Daytime migration, inland and coastal

Tracks of birds overland at *high altitudes* often are correlated with wind direction. In most cases, available evidence seems inadequate to distinguish whether the effect was solely due to pseudodrift or whether actual uncorrected drift was present[20,26,73,111,122]. However, in a few cases there seemed to be actual drift[16,68]. Except in soaring birds (discussed later), there is little firm evidence of drift compensation overland at high altitudes during the day, although compensation cannot be ruled out in the many cases where pseudodrift is a possibility.

In contrast, many European studies show that *low-altitude* overland migrants often compensate for drift. This is evident from a lack of correlation between tracks and wind direction[20,21]. In some cases there is a tendency to turn farther into the wind than necessary to compensate for lateral drift from the preferred heading[38,65,68,105,109,111,116,132]. This overcompensation is most common during the latter part of the daytime flight. Although some daytime studies have found evidence of either pseudo- or actual drift, most of these studies could not distinguish the two, and probably included high- as well as low-altitude migrants[58,67,117,126].

Thus, during the daytime, drift is apparently common only at high altitude; low-altitude migrants often compensate or overcompensate (turn upwind). These results are consistent with Alerstam's model predicting, for birds far from their destinations, high-altitude drifted flights followed by overcompensation at low altitudes where wind speeds are reduced[13-15].

The apparent rarity of uncorrected drift among low-altitude migrants (excluding soaring birds) is surprising, given that many migrants concentrate along coasts on days with crosswinds. It is widely assumed that this is due to lateral drift plus a tendency to follow coastal leading lines. However, even without overland drift, concentrations may occur at the coast because of 1) landward drift over the sea with onshore winds, and 2) the lower average windspeed overland, which induces birds flying in partly opposing offshore winds to remain along the shore[19].

Nocturnal migration, inland and coastal

Data on tracks and headings of nocturnal migrants relative to wind reveal no consistent pattern. Many studies have shown a correlation between mean tracks and wind direction. In most cases it is unclear whether this was caused by pseudodrift, incomplete compensation for lateral drift, or both[27,57,69,70,96,120,122,125,126,130,131]. Some studies provide evidence of at least partial compensation for lateral drift at night[23,25,32,103,117,131], perhaps even including compensation by some birds flying in cloud[61].

There is some evidence of uncorrected lateral drift by passerines migrating overland at night. One moon-watch study showed a closer dependence of tracks on wind direction than expected based on pseudodrift alone[124]. A ceilometer study suggested that compensation occurred only near a large river and not elsewhere overland[30]. Telemetry showed conclusively that *Catharus* thrushes migrating over central North America in spring flew on constant headings that were not adjusted for changing winds; however, these birds did tend to select altitudes where drift is mitigated[39,40]. Sparrows released aloft at night also seemed to depart on fixed headings[49]. These four studies were in areas with variable winds, and most birds probably were far from their destinations. In that situation, uncorrected drift may be a good flight strategy[13-15].

Many interpretation problems have been caused by difficulties in separating various species of birds at night. A few workers who could distinguish rather specific cohorts of migrants at night have found their tracks to be unrelated to wind direction, indicating full allowance for lateral drift[10,44,50,51,123,138]. However, caution is necessary in interpreting this evidence. During radar studies, cohorts that compensate are more likely to be recognizable, through their consistent tracks, than are cohorts whose tracks vary widely depending on wind. Thus, uncorrected drift could be more common than suggested by a simple tabulation of radar evidence. Additional telemetry studies would be valuable.

Thermal soaring

Soaring birds are often seen in greatest numbers along coasts and ridges under crosswind conditions. Many observers have assumed that this is caused by uncorrected wind drift, which may be unusually severe for birds that spend part of their time circle-soaring in thermals[97,98,128]. However, visual counts suffer from serious detection biases, and a few workers have suggested that soaring birds, like many other diurnal migrants, may correct for drift[11,75,99].

Thermals occur overland during sunny days, and typically consist of isolated bubbles of rising air that move downwind. While circling upward in a thermal, soaring birds necessarily travel approximately downwind at about the speed of the wind[77,78,128]. This 'drift' differs from that discussed above[77], since net airspeed for circling birds is near zero. Thus, during soaring the track vector is expected to equal the wind vector. Interestingly, some soaring hawks and cranes bias their upward soaring so as to maintain a slightly non-zero heading vector oriented into the wind, thus reducing drift while soaring[8,76].

With a crosswind, birds gliding away from one thermal in search of another might 1) head in their preferred direction and be drifted by crosswinds, 2) adjust their headings into the wind to compensate for drift during the glide, or 3) head further into the wind to adjust for drift during both the glide and the preceding circling climb. Birds using strategy (1) would drift far from the preferred track because drift during soaring would be added to that during flapping flight. With strategy (2), all drift would occur during the climbing phase, and total drift would be less than with strategy (1). Only strategy (3) would compensate fully for drift.

Strategies apparently vary. Visual and radar observations show that migration corridors of soaring birds can be displaced laterally at least by small distances[66,80,118]. Tracking radar data show that the broad-winged hawk *Buteo platypterus* makes little attempt to compensate for lateral drift while gliding [strategy (1)] even though it compensates partially while soaring in thermals[76]; these data were obtained far from the destination, so drift is predicted[13-15]. In contrast, some other hawks compensate at least partially while gliding[76,77,128] [strategy (2)]. Indeed, there are indications that *Accipiter striatus* and the crane *Grus grus* may overcompensate during gliding so as to correct for lateral displacement during both soaring and gliding[8,76] [strategy (3)].

Overwater migration

Almost all studies of the directions of overwater migrants relative to wind have found a correlation between daily mean tracks and wind direction. In most cases pseudodrift may account for at least part of the effect. However, in some studies pseudodrift is an insufficient explanation because of one or more of the following: the drift effect is too large, headings are significantly more variable than tracks, headings are constant regardless of wind, or for geographic reasons[18,71,85,88,104,106,119]. Alerstam[9] gives a quantitative review of pre-1976 cases. Uncorrected drift also seems likely in situations where the position of an entire narrow-front migration corridor over the sea shifts laterally with crosswind[27].

The above are all studies in which migrants were observed while they were in flight over the sea. Many other publications describe cases of overwater migrants, usually immatures, appearing on islands or coasts to the left or right of their normal migration routes with crosswinds blowing in that direction[59,81,84,90,129]. Although direct evidence about routes of these vagrants is rarely available, the preponderance of evidence suggests that most are drifted laterally by crosswinds while migrating over the sea.

Only a few studies have reported evidence of strong compensation for lateral wind drift by overwater migrants. 1) One possible case involved long-distance migrants approaching an island destination (Hawaii)[141], when they may use terrestrial landmarks to compensate at least partially for drift[14,35,109]. 2) Evans and Lathbury suggested that hawks crossing the Strait of Gibraltar are not drifted[54]. However, this interpretation is questionable[55,72]. Also, both at Gibraltar and in Kerlinger[74], terrestrial landmarks normally were visible. 3) Some cohorts migrating off the Massachusetts coast reportedly had near-constant tracks regardless of wind[44,103], and probably were far enough at sea to be offshore migrants. In contrast, in a nearby area along the Nova Scotian coast, tracks of most cohorts were correlated with wind direction[126].

If overland migrants normally detect and correct for drift using the relative motion of visible terrestrial features, as is suspected (see above), then it is understandable why few if any overwater migrants compensate fully for drift. Partial compensation may be possible by reference to wave patterns[18], but complete compensation while far at sea would require some other method for detecting either the wind or its effects on tracks. Birds that take off inland, compensating for drift, may maintain the same heading if they move offshore. If so, they would effectively compensate for drift as long as the wind remained constant.

Reoriented and redetermined migration: true navigation?

When birds drift laterally from their preferred headings, their routes are unpredictable and unlikely to be duplicated from one year to the next. However, some birds (even juveniles) drifted outside their normal route in one year use the normal route in later years[144]. Ringing data suggest that, within a migration, some drifted birds (including juveniles) change course and return to the normal migration route or destination[52,91]. If so, how is the drift recognized and the new course selected? Is true navigation required? True navigation is the ability, while in an unfamiliar area, to determine the direction of the destination.

This ability has been demonstrated convincingly in only a few bird species[47]. Immature birds en route to previously unvisited wintering areas are generally believed to lack this ability, and to fly on a standard heading even if displaced[47,108].

Reoriented migration occurs when birds change heading while aloft. For example, many passerines travel SW from Scandinavia across the North Sea during autumn nights. Near dawn some can still be offshore beyond sight of land. Many then reorient SSE, generally toward the mainland coast[34,36,87,95,101,139]. Most workers have suggested that this reorientation occurs after westward drift by SE winds. However, Myres[101] found no close connection with easterly crosswinds over the sea. Similarly, many autumn nocturnal migrants fly SW over the western Atlantic Ocean near Nova Scotia and New England. When they are still offshore at dawn, they often reorient to the NW or north, toward the North American coast, even when beyond sight of land. Indirect evidence suggests that many of these birds were drifted offshore during the night by NW crosswinds[3,22,100]. Although this is no doubt true in some cases, many passerines migrate SW over the sea at night and reorient NW at dawn even without crosswinds[120].

Diurnal migrants often overcompensate after several hours of flight in crosswinds (see above). This is also a type of reoriented migration.

Redetermined migration occurs when birds initially fly on one heading, land, somehow recognize that they have been displaced from their preferred route, and then fly on a compensatory 'redetermined' heading during the subsequent flight. The distinction from reoriented migration within a single flight may be largely semantic when redetermined flight commences soon after the first flight ends. For example, inland in the southeast USA, some landbirds apparently are drifted laterally from preferred SW or NE headings at night. They may land before dawn but then depart on compensatory NW or (rarely) SE flights soon after dawn[57].

Most evidence of redetermined migration at longer intervals is inconsistent and weak. A thrush followed for six nights did not change heading to compensate for drift incurred during previous nights[39]. A few radar studies have revealed departures of nocturnal migrants that might be birds on redetermined migration after earlier wind drift[34,82], but other radar studies have provided little evidence of this[95,101]. In any case, these data are equivocal: the identities and previous movements of birds detected by radar are unknown, and there can be other reasons for movements in unusual directions[125]. Helbig et al.[68] reported stronger evidence of redetermined migration. One day after days with crosswinds, headings of diurnal migrants tended to be deflected toward the side from which the crosswind had been blowing. This phenomenon is similar to overcompensation, but fits the definition of redetermined migration because of the 1-day delay.

Evans[52] studied certain Scandinavian passerines that had apparently been drifted west of their normal autumn route while flying over the North Sea. Both when tested in cages and when subsequently released, they oriented SSE rather than in the assumed preferred direction (SSW). Also, ringing data showed that some drifted birds returned to their normal route. Although these data suggest that nocturnal passerine migrants (including juveniles) can redetermine their headings after drifting outside the normal autumn migration route, replication of this study was needed[47]. No direct replication has been reported, but the most comparable study found no evidence of redetermined orientation[114]. Other work by Rabøl provides indications that some displaced autumn migrants can redetermine the bearing toward points along the migration route[112], but the results are variable and controversial[47]. There is better evidence of redetermined migration of drifted migrants in spring, when all age classes are returning toward a known destination[91]. Evans, Rabøl, and various reviewers[4,47] have noted that reoriented and redetermined migration, even by immatures, may be possible without a true navigation ability. Wind drift could be perceived in other ways (see above), and at least a rough compensatory compass response or upwind flight could then be made. Dawn reorientation by landbirds over the sea could be a compass response adapted to the general alignment of the coast near their migration route.

Several cases of reoriented and redetermined migration are consistent with the drift vs compensation strategies discussed by Alerstam[13-15]: 1) Some cases may be compensatory flights at low altitude following lateral drift at higher altitude[3,22,57,68]. 2) The frequency of dawn reorientation over the North Sea is highest in late autumn, when short-distance migrants predominate[86]. 3) In autumn, nocturnal migrants that resume flying in the daytime do not seem to redetermine their headings after drift in the northeast USA[29,30] but do so farther south[57] where the majority are presumably closer to their destinations.

Wind as a directional cue

If birds can sense wind direction when flying or before takeoff, wind might be useful in maintaining or even selecting a heading. Birds often fly directly downwind or upwind, and in a few cases they may be reacting to wind direction itself. During active down- or upwind flight, there is no lateral wind drift; tracks and headings are equal. Birds might also maintain another angle (besides 0° or 180°) relative to wind direction.

Selection of heading

Emlen[47] suggested that some birds might take off when various weather variables indicate the presence of a weather pattern with following winds relative to the preferred heading, and then orient downwind. This might provide 'a crude means of selecting as well as maintaining a direction in the absence of celestial, magnetic or inertial information'[47]. Many studies show a preference for flight when winds are roughly following[121, 127]. However, few of these cases represent downwind orientation: variation in headings and tracks usually is less than variation in the wind directions during those flights. Even so, some birds may orient relative to wind when other cues are absent.

The southeast USA is one area where downwind orientation may be common among passerine migrants on both clear and overcast nights[1, 56]. Mean tracks and headings were downwind regardless of wind direction, even though wind speeds were usually low enough to allow flight in other directions. Numbers aloft varied widely in relation to weather, but the few passerines flying with north winds in spring or south winds in autumn flew downwind in seasonally inappropriate directions. Thus, these birds seemed to use wind as their primary directional cue. The adaptive value of some aspects of this behaviour is unclear[1].

Although the tendency for downwind flight is unusually strong in the southeast USA, some studies elsewhere show a strong downwind component when all cohorts of migrants are pooled[126]. However, studies elsewhere indicate that specific cohorts do not orient consistently downwind. Also, even in the southeast USA some studies[57, 96] suggest less consistent downwind orientation (cf.[1, 56]). Tracking radar and telemetry studies in the southeast USA are desirable to provide more precise data on reactions to wind there.

Williamson interpreted the arrival of many vagrant birds on the British coast as evidence of *downwind directed drift*[142, 143]. He believed that, when overwater migrants become disoriented in fog, cloud and rain (as can occur)[44, 87, 89], they reorient and fly actively downwind, possibly observing waves to determine wind direction. Over landlocked seas like the North Sea, this strategy might reliably bring the disoriented bird to shore rather quickly. However, evidence of 'downwind directed drift' is indirect at best, and was discounted by Lack[83, 84, 87, 90]. He showed that most cases can be explained in other ways, e.g., uncorrected lateral drift over the sea. However, both Lack and Evans[50] conceded that active downwind flight over the sea cannot be totally discounted.

Reminiscent of Williamson's hypothesis were Able's findings[6, 7] that some nocturnal landbird migrants switch to downwind orientation when overcast hides celestial cues. Migrants over central New York State did so even when this took them in seemingly inappropriate directions. Sparrows whose form vision was blocked by opaque contact lenses also headed roughly downwind when released aloft at night. This indicates both an ability to sense wind direction by non-visual means and a preference to fly downwind when visual cues are absent. Again, the adaptive significance of this behaviour is uncertain. Also, these results seem inconsistent with other evidence showing that nocturnal migrants often do not orient directly downwind when under or even in overcast, e.g.[48, 61, 126].

Maintenance of heading

Vleugel[133–135] suggested that some migrants select a heading using one directional cue, e.g., sunrise or sunset, and maintain that heading by flying at a constant angle relative to wind direction. His evidence included indications of reduced migration when the wind was calm or variable, and changes in tracks when there were corresponding changes in wind direction. This evidence is questionable because of detection biases and the likelihood that different cohorts of migrants were observed at different times. Also, some of the changes in tracks as wind changed may have been overcompensation for drift. Bellrose[23, 25] also felt that migrants often maintain their headings using the wind; his data were also circumstantial. However, despite the lack of good evidence, the hypothesis may apply in some cases[60].

Vleugel assumed that birds could only sense the wind direction by reference to the landscape[133] or possibly the 'cloudscape'[137]. However, if birds can sense wind direction by a non-visual method[7], orientation relative to the wind could be even more useful than Vleugel suggested.

Upwind orientation

Some species often migrate more-or-less into the wind, often at low altitude. No doubt many of these birds orient using directional cues other than wind. However, some of these flights – those including overcompensation for previous lateral drift – are partly directed by the wind. Rabøl[109, 110] suggested that many diurnal migrants have a more specific preference for flying upwind. For most species this is unproven[37] and unlikely on energetic grounds[11, 14, 121]. However, swifts and swallows often head directly into the wind during long-distance flights (reviews[45, 121]; also[11, 94]). The reasons are speculative but in any case these birds seem to orient specifically into the wind.

Downwind motion with no net airspeed

While circling in a thermal, soaring birds generally 'drift' downwind along with the thermal (see earlier). Also, birds that are disoriented and milling in poor visibility have, on rare occasions, been reported to drift downwind at the speed of the wind[44, 87, 90]. In these cases, birds are carried passively by the wind; wind direction is not a directional cue.

Conclusions and prospects

Two decades ago some workers thought that most passerines compensate almost totally for lateral drift[50, 65, 103]. This would minimize the need for complex navigational abilities. However, even then it was recognized that variable reactions to wind could be selectively advantageous[50, 52, 65, 101].

It is now obvious that migrants have many adaptations to deal with the profound effects of wind on their flights. Migration past an observation point is a variable mixture of birds that do and do not compensate for lateral drift. In addition, wind selectivity causes pseudodrift, which further complicates interpretation[32]. We are beginning to find a few patterns in this variable behaviour[11–16, 18, 19]. It now appears that optimum behaviour may range, depending on circumstances, from total tolerance of drift to total compensation. Some birds may require less time and energy for migration if they tolerate uncorrected wind drift at certain times.

Birds that tolerate wind drift will necessarily follow unpredictable routes. The low recurrence rates of most types of birds at en route trapping stations are consistent with this. However, the fidelity of many species to breeding and wintering areas indicates that the terminal phase of migration must often be less dependent on the vagaries of wind. Drift is reduced by selecting flight times (and sometimes altitudes) with minimal crosswind[39, 40], plus active compensation for drift in some situations. When birds are displaced laterally by wind, overcompensation, reorientation, and redetermined migration seem to provide important compensatory mechanisms, apparently in some juveniles as well as adults[3, 52]. In theory, many of the known examples of compensation could occur without a true navigational ability. However, the actual orientation processes involved are uncertain.

Much additional information about flight strategies is needed. Traditional field observation methods can still be useful. However, studies using tracking radar, releases aloft, and especially telemetry will be especially valuable. Use of telemetry to follow known individuals through variable environmental conditions over one or more nights can provide uniquely valuable data[39, 40]. These types of studies will also be needed to determine whether some birds maintain or select their headings using wind as a cue. Further study of the ways in which birds sense wind direction, especially at night, over the sea, and in poor visibility, are also needed. Additional experimental work on captive displaced migrants is needed to help resolve the orientational mechanisms used to compensate for drift.

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