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Birds: blowin' by the wind?

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Abstract Migration is a task that implies a route, a goal and a period of time. To achieve this task, it requires orientation abilities to find the goal and energy to cover the distance. Completing such a journey by flying through a moving airspace makes this relatively simple task rather complex. On the one hand birds have to avoid wind drift or have to compensate for displacements to reach the expected goal. On the other hand flight costs make up a large proportion of energy expenditure during migration and, consequently, have a decisive impact on the refuelling requirements and the time needed for migration. As wind speeds are of the same order of magnitude as birds' air speeds, flight costs can easily be doubled or, conversely, halved by wind effects. Many studies have investigated how birds should or actually do react to winds aloft, how they avoid additional costs or how they profit from the winds for their journeys. This review brings together numerous theoretical and empirical studies investigating the flight behaviour of migratory birds in relation to the wind. The results of these studies corroborate that birds select for favourable wind conditions both at departure and aloft to save energy and that for some long-distance migrants a tail-wind is an indispensable support to cover large barriers. Compensation of lateral wind drift seems to vary between age classes, depending on their orientation capacities, and probably between species or populations, due to the variety of winds they face en route. In addition, it is discussed how birds might measure winds aloft, and how flight behaviour with respect to wind shall be tested with field data.

Keywords Bird migration · Flight behaviour · Flight costs · Wind drift · Wind influence · Migratory strategies

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Introduction

Bird migration necessitates the ability to arrive at a destination hundreds or thousands of kilometres away within a limited time span. To accomplish this task, the migratory bird requires orientation abilities to find the goal and the necessary fuel for the flight engine in order to cover the distance. Migratory behaviour moulded by environmental and endogenous factors determine the two stages of migration, stopover and flight (Jenni and Schaub 2003).

Energy, time and safety have been promoted to be the major parameters responsible for survival and fitness consequences during migration (Alerstam and Lindström 1990). Although there is more energy and time spent during stopovers, flight efficiency is a key factor for the overall time and energy requirements during migration. Flight costs determine the necessity for fuel accumulation during stopovers. The flight route is decisive within the context of total migratory distance, the potential of favourable stopover sites en route and the risks aloft and on the ground and, therefore, in determining the overall energy and time dispensed during migration and the safety of the migration.

Obviously, the highly dynamic atmosphere has an important impact on all aspects of a bird's migratory flight (Alerstam 1990). Wind speed, which lies in the same order of magnitude as the bird's own airspeed, can easily double or half a bird's speed over ground and, correspondingly, the costs of transport. Lateral wind drift must be compensated for immediately by heading into the wind, otherwise the flight route will be shaped by the wind conditions experienced en route. Hence, a migratory bird should be able to detect the varying wind forces aloft and react adequately to either profit from the wind factor or at least avoid costly wind effects.

Since the reviews of Richardson (1978, 1990a, b, 1991), numerous studies have been published on how birds should or actually do react to winds aloft. The objective of this article is to summarize the theoretical

and empirical studies that have been carried out during the past 15 years on the flight behaviour of migratory birds in relation to the wind. Some of the theoretical investigations that have attempted to shed some light on how birds may detect wind are also discussed.

Wind characteristics

When viewed on a large scale, wind patterns are well known, and there are regions and times for which wind conditions are highly predictable (Fig. 1). Wind patterns are essentially mirrored at the equator, but as land-masses, in particular, have a distinct impact on the distribution of high- and low-pressure centres, winds are more variable in the northern than in the southern hemisphere. Above land, wind speeds are usually weaker than above the sea and, in general, wind speeds increase with altitude. While long-term regional means are well-defined, short-term local predictions are often difficult and unreliable. In many cases, the small-scale winds are highly variable in time and space, specifically among the northern and southern mid-latitudes through which high- and low-pressure centres pass frequently (Walch and Frater 2004). These substantial differences in large-scale predictability and small-scale variability make it tricky to evolve general behavioural rules to cope with current wind conditions. The potential displacement a bird might experience can vary considerably along its migratory route (Fig. 2). At almost any site, there is a chance of encountering some favourable winds, but their rate depends strongly on the time and the altitude selected for the migratory flight. While take-off from one stopover site might highly depend on the rare occurrence of favourable or at least weak winds (Fig. 2a), it might be independent of wind at a site where tail-winds are available regularly, at least at a specific flight altitude (Fig. 2c). It is therefore dependent on the individual bird's capabilities to choose the appropriate time and flight altitude for its migratory journey, always bearing in mind the entirety of the migration (e.g. time restriction, risk avoidance, etc.).

As a consequence of the variability of winds along the different migratory routes, behavioural adaptations may be indispensable for one flight route, but negligible for another. Stable and predictable conditions may entail strong selection pressure on behavioural adaptations (genotypic selection) that would enable the migrant to make use of a reliable energy source. Changing conditions may, in contrast, favour other specific adaptations (e.g. phenotypic plasticity) promoting flexible reaction norms, thereby entailing rules of thumb based on unreliable sources of information. Therefore, any analysis of wind influence on migration has to consider the specific conditions; for example, if favourable winds are always available at some flight altitudes (trade wind zone), there is no need to choose a specific time for take-off, but an efficient wind detection aloft would be required.

Wind detection

Behavioural adaptations to environmental conditions are constrained by the ability of a bird to perceive the relevant features. To estimate wind aloft, a bird must be able to detect both its direction and speed with respect to the ground and then to put it into relation with an expected direction and speed under calm winds. It seems reasonable that a bird “knows” its airspeed based on its common power consumption and his preferred flight direction according to its orientation skills (Wiltshko and Wiltshko 2003). To date, no direct experimental studies of how birds can detect wind movements have been carried out. However, mechanoreceptors at or near the feather follicles in the wings are sensitive to the magnitude of airflow over the wings (Brown and Fedde 1993). These mechanoreceptors will provide information on wind speed as long as a bird is sitting on the ground, but not while flying. However, once the bird is aloft, these sensors will provide a clue on airspeed instead. Aloft, birds seem to use visual landmarks to take into account wind displacement (Richardson 1990a, b and references therein). The use of small-scale air turbulences, as measured by wind profiler radars, have been discussed (Elkins 1988), but as a bird is moving with the air it seems to be unlikely that birds detect these turbulences with enough accuracy to measure wind speed and direction aloft. Since the publication of

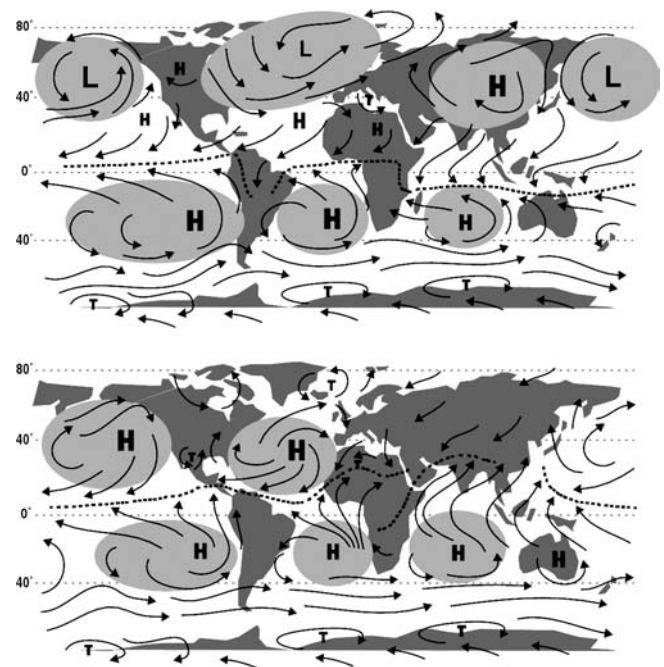
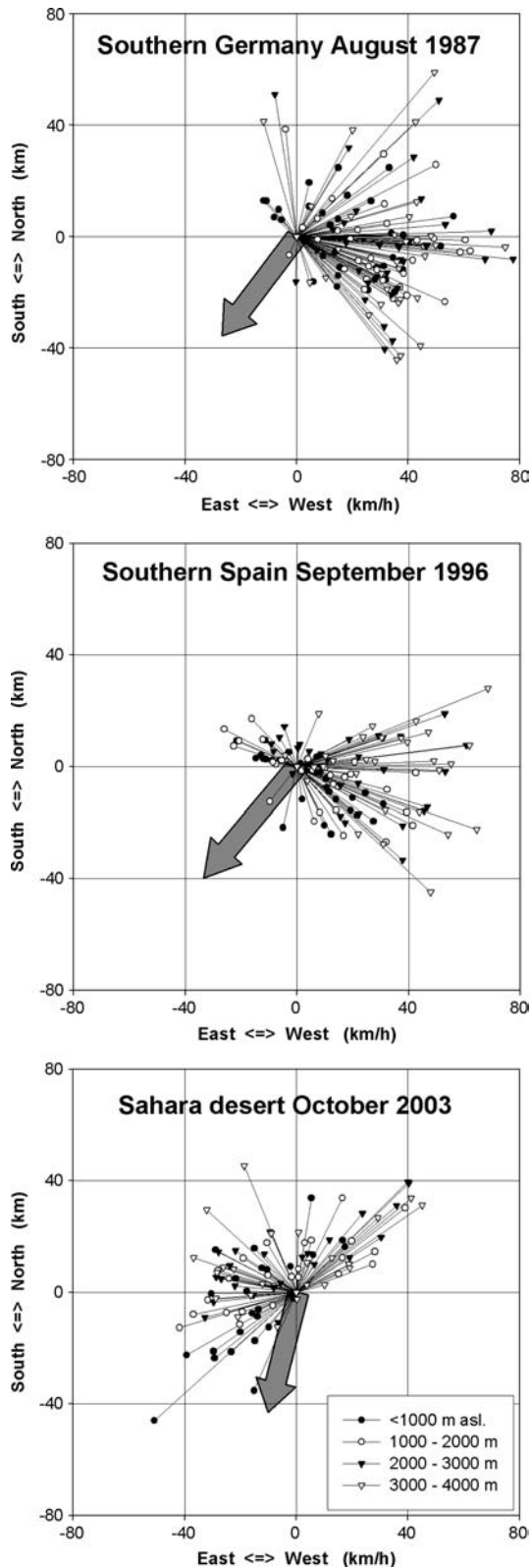


Fig. 1 Global distribution of the average main pressure centres and wind patterns during northern winter (*above*) and summer (*below*) conditions. High- (*H*) and low- (*L*) pressure centres are indicated as *light-grey areas*, wind patterns as *arrows* (S. Bader, MeteoSchweiz, personal communication)



◀
Fig. 2 Distribution of the potential wind displacements at three sites along the western African-Palaeartic flyway. *Lines with symbols* give the distance of the average displacement per hour by the wind for four different altitudes. *Values* represent means per night and height intervals. The *arrows* indicate the mean flight directions and ground speeds of nocturnal passerine migration (wing beat frequency > 12.5 Hz) measured by tracking radar at the respective sites (Nievergelt et al. 1999 and unpublished data; $n = 319, 326, 415$, respectively)

A simple method to determine the angle between body axis (heading) and flight direction is to watch the pattern in angular velocity of landmarks to the left and the right. Maximum angular velocity will always be right-angled to the flight direction, irrespective of the heading of the bird. Thus, with no lateral drift, the maximum angular velocity of the landmarks is reached just at the right angle to the body axis on both sides (Fig. 3). With increasing lateral wind drift, maximum angular velocities are shifting in opposite directions – on the lee side landmarks in front of the bird are moving the fastest, while on the luff side the landmarks behind the bird are moving fastest. This phenomenon fits in well with a peculiarity in the bird's vision. Various studies have shown that birds do have a large lateral view and preferentially fixate distant objects in their lateral view (Güntürkün 2000). This characteristic would allow birds to estimate wind displacements quickly by considering the difference in the motion patterns of landmarks to the left and right, without the necessity of inspecting the movement of a single landmark in detail. Consequently, based on the overall movement of landmarks, a bird would then be able to estimate its speed with respect to the ground. However, this movement, the angular speed of landmarks, depends not only on ground speed but also on the distance to the landmark and, therefore, the flight altitude. At a constant ground speed, the angular speed of a given landmark decreases rapidly with increasing flight altitude. Under calm wind conditions and constant ground speed, the angular velocity decreases smoothly with altitude. The addition of a theoretical but nevertheless realistic wind profile to the bird's air speed (head- and tail-winds) generates a distinct pattern with abrupt changes in angular speeds in which ground speed reaches minima and maxima, respectively (Fig. 4). We would therefore expect the highest migratory densities at the lowest local maxima. However, as no studies have yet been carried out to determine to what extent a bird might sense variations in angular velocities, we only can speculate that birds may use these distinct changes to detect favourable altitudes.

If visual cues on the ground are used to detect wind, we expect appropriate corrections to winds aloft to decrease with flight altitude and visibility of landmarks (Liechti 1993). However, lack of compensation at high altitudes also coincides with Alerstam's assumption (1979b) that birds allow themselves to be drifted at high altitudes but compensate for this displacement during low-flight altitudes (see below).

Richardson's reviews (1990a, b), there has been no new empirical evidence reported on whether birds use anything else than visual cues for estimating wind conditions aloft.

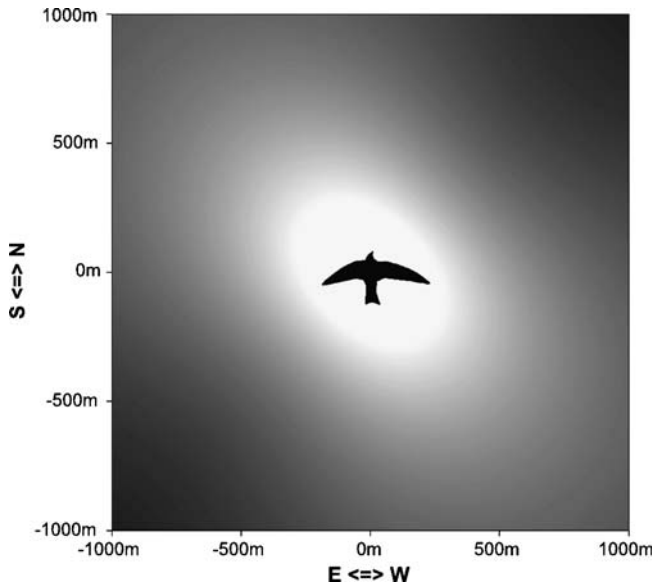


Fig. 3 Relative movement of the topography is shown as the angular speed of a point on the surface with respect to the flying bird. The bird is flying at 500 m above ground level at 10 m/s (ground speed) heading into the wind at an angle of 45° . The shade of grey ranges from <0.1 to $>1.2^\circ/\text{s}$

Pennyquick (1989) pointed out that decreasing or increasing air speed with respect to tail- and head-winds can reduce flight costs considerably. If the detection of ground speed and lateral drift is estimated separately by the bird – i.e. a bird would only consider angular speed for ground speed estimates – strong lateral winds resulting in high-ground speeds would induce the same adaptive effect as tail-winds.

Departure decision

Apart from precipitation, wind is the most important weather factor affecting the departure decision of migratory birds (see Richardson 1978, 1990a and references therein). Generally, strong head-winds weaken a bird's propensity to take off (Battley 1997) and can promote an accumulation of birds ready for take-off ("Zugstau"). In contrast, weak winds and tail-winds promote take offs (Pyle et al. 1993; Gudmundsson 1994; Baumgartner 1997; Gauthreaux and Belser 1999; Green et al. 2002; Schaub et al. 2004). However, Thorup et al. (2004) found no effect of wind selectivity for the osprey *Pandion haliaetus*, assuming that diurnal migrants, which cannot use stopover time for efficient foraging are less prone to wait for favourable winds. Long periods of harsh weather conditions can force birds to depart from a site even under head-winds (Bolshakov and Rezvyi 1998; Erni et al. 2002; Jenni and Schaub 2003). On the other hand, at sites where tail-winds are always available at a specific height (e.g. trade wind zone) an effect of the wind on departure decision may be absent at all (own unpublished data).

Several models based on the time and energy minimization theory have been presented to predict optimal stopover duration and, thus, departure decisions (Alerstam and Lindström 1990; Weber et al. 1994, 1998b; Weber and Houston 1997; Hedenström and Alerstam 1997; Chernetsov et al. 2004). As wind plays a key role in energy and time expenditure per unit distance covered, it is not surprising that several field studies scarcely mimicked model predictions when wind was not considered (Lindström 1991; Dänhardt and Lindström 2001; Chernetsov et al. 2004). Liechti and Bruderer (1998) demonstrated the importance of wind for an optimal departure decision which Weber et al. (1998a) and Weber and Hedenström (2000) subsequently included in their model predictions. The differential use of stopover sites in relation to wind conditions (i.e. skipping stopover sites) was found by Beekman et al. (2002) in Bewick Swan (*Cygnus bewickii*) migration.

However, it is still unclear how birds judge wind conditions aloft while sitting on the ground. Although surface winds are correlated with winds aloft (see Baumgartner 1997), wind speed is generally reduced on the ground, and direction can be considerably deflected by local topography. Typically, pressure changes are related to specific changes in wind conditions aloft (Richardson 1982; Alerstam 1990), and birds seem to rely regularly on these pressure changes. Several studies have found a good correspondence between departure decisions and the pressure changes related to an approaching cold front (Dau 1992; Richardson 1990a;

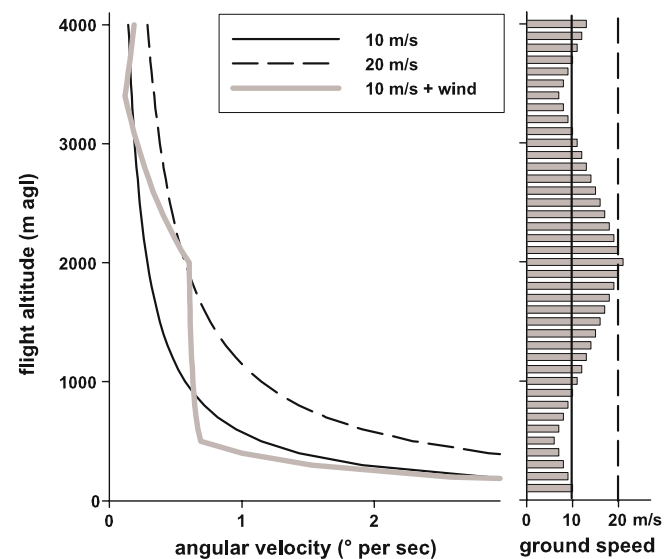


Fig. 4 Decrease in the angular motion of a landmark just vertically below the bird; thus, the maximum angular velocity for a given ground speed. Examples are given for the angular velocities of a landmark vertically below a bird in relation to flight altitude and different ground speeds. The left graph shows the change in angular velocity with altitude for three theoretical examples. The right graph shows the corresponding ground speeds. The grey bars correspond to the thick grey line (left) and indicate the change in ground speed due to varying wind conditions

Zehnder et al. 2001). However, birds may even take off under any wind condition to perform exploratory flights to check for favourable winds aloft. In view of this, we should expect to find premature flight interruptions under conditions of unfavourable winds, but to date there is very little published data available on this aspect.

Flight altitude

Apart from topographical aspects – that is, the vertical profile of the earth's surface – flight altitude can be chosen almost freely by a migratory bird. Several observations have confirmed that birds can actively fly at heights up to 8 km above sea level (a.s.l.) (Stewart 1978; Williams and Williams 1978; Liechti and Schaller 1999). Even small passerines can fly regularly at heights up to 4 km a.s.l. (Richardson 1991; Bruderer and Liechti 1995; Gauthreaux and Belser 1999; Williams and Williams 1999; Lensink et al. 2002).

Flying at high altitudes in low-air density reduces the cost of transport at an increased air speed (Pennycuik 1978), whereas water loss generally increases with altitude, mainly due to an increased respiration volume (Carmi et al. 1992). In addition, climbing can make up an important proportion of the energy expenditure, mainly in large birds and for short flights (Hedenström and Alerstam 1992), with the exception of thermal soaring migrants. Thus, even in still air, for each individual bird there is an optimal flight altitude with respect to energetic and physiological aspects. However, as still air throughout the entire airspace of a bird's potential flight altitude is very rare, a bird is almost always confronted with different airflows in space and time. Being aware of the wind, a bird may choose an optimal flight altitude with respect to the energy, time and/or water budget.

Various authors have mentioned that migratory birds are selective for flight altitudes with favourable winds (Richardson 1978, 1991; Gauthreaux 1991 and references therein). Bruderer et al. (1995) successfully predicted distributions of flight altitudes based on the assumptions that birds explore winds at different heights and choose flight levels according to differences in wind support between neighbouring levels. Further models investigating optimal flight altitudes with respect to minimizing energy consumption or water loss, found a profound effect of wind (and thus energy), but no clear support for a water-driven altitude selection (Klaassen and Biebach 2000; Liechti et al. 2000). Recent data from Sahara desert crossings corroborate the priority of wind support relative to that water balance (F. Liechti and H. Schmaljohann, unpublished data): in the autumn, the vast majority of passerines crossing the Mauritanian desert preferred to fly at flight levels below 1000 m above ground level (a.g.l.) with a considerable tail-wind, while based on the model predictions the hot (> 30°C) and dry (< 20% relative humidity) air would imply much higher water losses at low altitudes than at high

ones. Studies from the arctic region have revealed that flight altitude may also depend on the length of the actual flight stage. Birds heading for a long-distance flight across the pack ice or the North Atlantic ocean (Richardson 1979; Alerstam and Gudmundsson 1999) chose considerably higher flight altitudes than birds crossing the Northwest passage in Canada, these latter having countless occasions for a stopover (Gudmundsson et al. 2002). As the high-flying birds had much more wind support than those at lower levels (< 1000 m.a.g.l.), wind might still have been the major factor for the choice of the flight altitude. If the length of a flight stage has an impact on the bird's flight altitude, we can assume that the climbing costs play an important role. Thus, we would expect small birds with relatively low-climbing costs (Hedenström and Alerstam 1992) to explore higher altitudes more frequently than large birds when both are taking off for similar flight distances. Large birds using powered flight for migration (e.g. swans) might be restricted in flight altitude as a result of limits in climbing performance (Pennycuik et al. 1996, 1999).

Flight altitudes up to 4 km must be regarded as common. Therefore, many studies that have investigated the seasonal or diurnal course of migratory intensity with inadequate methods, i.e. not covering the main height ranges of migration (e.g. visual observations that can cover hardly a few hundred meters), should be viewed with great caution.

Flight direction and speed

Once aloft the bird's air speed and heading together with the wind vector determine its flight speed and flight direction. Having chosen a flight altitude to benefit from favourable winds, a bird can minimize energy consumption per unit distance by flying at maximum range speed but it can also adapt heading to minimize the remaining distance to a specified goal (Pennycuik 1989; Liechti 1995; Alerstam and Hedenström 1998). This requires not only an estimate of wind speed and wind direction but also a clue of the distance and direction to the goal. As many birds return every year to the same breeding and wintering site (see Glutz von Blotzheim et al. 1971; Salewski et al. 2000), it is indispensable that they compensate for wind drift both coming and going. Compensating completely for the actual lateral drift has the advantage that a bird must not reorient during its subsequent migratory journey – i.e. a vector navigation program (Schmidt-Koenig 1973) would be sufficient to arrive at the specified goal. Allowing lateral drift would imply either true navigation (Gwinner 1971) or the ability to remember experienced drift and compensate for it during a subsequent flight stage (Gauthreaux 1978; Rabol and Thorup 2001), or the toleration of a displacement from the goal.

In theory, optimal drift compensation is dependent on the expected wind conditions en route and the

remaining distance to the goal (Alerstam 1979a). Under stable wind conditions full compensation is the optimal behaviour, while under variable, unpredictable winds adaptive drift strategies would save time and energy for the migratory journey (Alerstam and Hedenström 1998). As a rule of thumb, migrants should allow drift at the beginning of the journey and increase the amount of drift compensation with decreasing distance to the goal; additionally, they should allow lateral drift under strong winds (at high altitudes) and compensate for it under weak winds (at low altitudes).

Demonstrating whether migrants do or do not compensate for wind drift during flight is not a simple task, as in many field studies we do not know the goal of the birds in question. Directional behaviour is generally analysed by comparing track and heading directions under different wind conditions. Green and Alerstam (2002) critically analysed the methods used in the past to investigate whether migrants drift with the wind or compensate for drift. The major problem in statistical analysis of field data is the non-random distribution of winds. Their results showed that the methods adopted for comparing individual tracks can yield strong biases, resulting in false conclusions. Their simulation analysis illustrated clearly that the lack of a uniform – or at least random – distribution of wind directions (which is normally the case in field studies) produces significant spurious correlations. As a robust method they recommended that the mean geographic track and heading direction of a migratory movement (e.g. within a night) for occasions with different wind conditions be regressed with the angle between track and heading. This allows not only drift and compensation to be distinguished but also enables a statistical analysis of the amount of drift and compensation, respectively, to be carried out. However, we still must keep in mind that in many studies in which the goal destination for the migrants tracked was not reasonably identified, a significant wind drift could be due to pseudodrift; i.e. that bird populations with different goal directions choose different wind conditions to migrate (Evans 1966; Nisbet and Drury 1967; Alerstam 1978).

Richardson (1990b) summarized several studies showing complete compensation as well as partial and full drift. Complete compensation was often linked to diurnal migration (Brodeur et al. 1996; Alerstam and Gudmundsson 1999; Green et al. 2003), while partial or full drift was found in nocturnal migrants (Hilgerloh 1991; Liechti 1993; Gudmundsson 1994; Zehnder et al. 2001). Adaptive drift compensation – i.e. the compensatory behaviour varying according to different factors (Hedenström et al. 2003) – was confirmed in a few studies (Bäckman and Alerstam 2003; Green et al. 2004; but see Green 2001). Desholm (2003) assigned small-scale changes in flight direction at least partly to wind drift compensation.

Based on satellite tracks of ospreys and honey buzzards (*Pernis apivorus*), Thorup et al. (2003) found a distinct age-specific difference with respect to compen-

sation of wind drift. Juveniles, as probably vector-oriented individuals, did not compensate for lateral wind drift, while adults, as goal-oriented migrants, compensated partially for lateral wind drift, as would be expected in an adaptive drift strategy. This result, which is in line with Perdeck's (1958) famous experiments with starlings, indicates that juveniles might actually be unable to adopt a goal-oriented adaptive drift strategy. However, even if the latter is true, it does not rule out that juveniles are equipped with some drift avoidance and drift compensation rules. Following distinct topographical features close to the preferred migratory direction is well known as the leading line effect (Williamson 1962; Bruderer 1978). Heading into the wind irrespective of its strength was observed in nocturnal songbird migration in a population dominated by juveniles (Liechti 1993). The selectivity for favourable winds (departure, altitude) is another important aspect in avoiding potential wind drift.

Irrespective of orientation, wind support affects the optimal air speed which the bird adopts to achieve a maximum range with a given fuel load (Pennycuik 1978; Liechti et al. 1994; Hedenström and Alerstam 1995). According to theoretical predictions, birds should increase air speed in head-winds and cross-winds and decrease it in tail-winds. The predicted increase in air speed with increasing head-wind and decreasing tail-wind, respectively, has been established in a few studies (Liechti 1992, 1995; Spear and Ainley 1997; Alerstam and Gudmundsson 1999; Hedenström et al. 2005). One method used to demonstrate this effect was to plot the difference between air speed (V_g) and ground speed (V_a), $V_g - V_a$, versus the air speed (V_a). It is obvious that these two variables are not independent, and this can produce spurious correlations. There is no space here to discuss this problem in detail, however, Figure 5 gives an example of the potential bias introduced by using this measure for a wind effect. Although there should be no wind effect (no varying winds), there is a clear negative correlation between V_a and the wind effect ($V_g - V_a$). To what extent this effect has influenced some of the results in earlier studies has to be investigated elsewhere. An increase in air speed with increasing cross-winds has not been confirmed to date (Hedenström et al. 2005). In the case in which the detection of ground speed and lateral drift is estimated separately by the bird – i.e. a bird would consider only angular speed for estimating ground speed (see above) – strong lateral winds inducing high ground speeds would have the same effect as a tail-wind; thus, a bird might react opposite to the predictions and air speed might be reduced in cross-winds. The main obstacle to clarifying this question properly is a technical one: a sample of flight tracks of birds known to compensate completely for lateral wind drift is required. Long-distance tracking has been accomplished using radio telemetry (Cochran 1972). High-resolution satellite tracks should provide the opportunity to test these predictions.

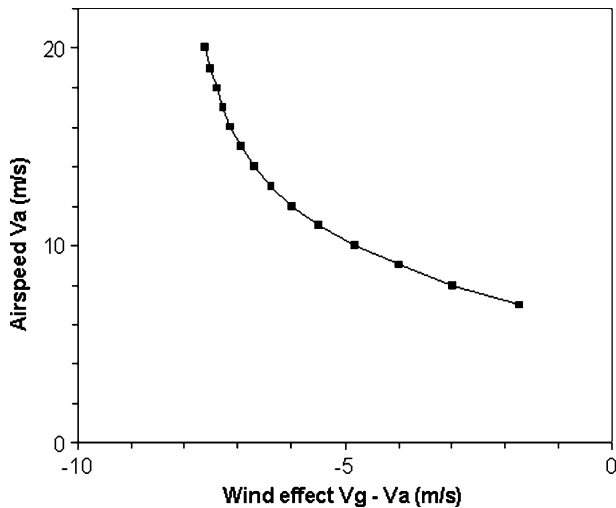


Fig. 5 Relation between airspeed (V_a), and the so-called wind effect, airspeed – ground speed ($V_g - V_a$) for a selected range of airspeeds (7–20 m/s). Wind direction (30°) and wind speed (10 m/s) are kept constant. The example shows that if there is any variability in the airspeed within a given sample of tracks, a spurious correlation emerges even under constant wind conditions

Large-scale view

Some of the migratory flyways seem to be a consequence of the general airflow around the globe. Flights across the West-Atlantic ocean and the Pacific or across the Sahara seem to be strongly aided by reliable tail-winds (see Piersma et al. 1990; Williams and Williams 1990; Butler et al. 1997; Clark and Butler 1999; Piersma and Lindström 2002). The prevailing winds seem to be a necessity for the successful journeys of several populations of long-distance migrants (Gill et al. 2005). Erni et al. (2005) have modelled the different aspects of a whole migratory journey (departure/flight stages/stop-over; fat accumulation/barrier crossing). Their simulations propose that a vital significance be given to the selective use of favourable winds as a means of explaining the current pattern of migration from Europe to sub-Saharan Africa (see Clark and Butler 1999).

Recent studies have analysed the effect of large-scale weather phenomena, such as the winter North Atlantic Oscillation index (NAO), on the timing of spring migration (Forchhammer et al. 2002; Hüppop and Hüppop 2003; Vähätalo et al. 2004). All found a significant relation between the NAO index and the timing of spring migration. However, we have to be aware that the relevant factors sensed by the birds are variations in, for example, temperature and/or wind conditions (Hüppop and Hüppop 2003). A shift in one of the major pressure centres may be beneficial for migrants flying towards one region, while it may be detrimental for others flying towards another region.

Very little is known about the impact of occasional storms on survival during migration and flight routes. Butler (2000) found some evidence that the number of stormy days during migration might influence the

abundance of breeding birds. I propose that we should consider placing much more weight on this kind of risk, as it probably far outweighs the risk of predation.

Perspectives

Short-lived birds perform the migratory journey at most only a few times during their lifespan, and their migratory strategy may mainly be based on an endogenous programme and have adequate reaction norms. Long-lived birds may improve their migratory strategy with increasing experience (Thorup et al. 2003). In addition, social birds can profit from experienced individuals and build up migratory traditions including the use of reliable winds (Schüz 1971).

Bird migration has evolved along with long-term climate changes. With respect to the recent climate change, I suspect that populations confronted already with a high variability in environmental conditions might become accustomed more easily to new conditions, as their set of reaction norms is large and thereby enables a gradual adaptation to the new conditions. Populations still migrating along stable and reliable conditions may suffer more in the future as they possibly have to evolve a specific behavioural trait to cope with the new conditions.

How are these behavioural traits implemented in the migratory strategies? How do juvenile birds know that they have to check winds? Is there a specific inherited programme, or do they just have the cognitive opportunity to learn from the actual environment? How is their range of reaction norms, when confronted with new wind situations, and do they learn to deal with the wind?

Simulation models validated with empirical data are helpful tools by which to learn more about the underlying processes. To build up appropriate models, it would be valuable to know how birds detect winds aloft. Very little is as yet known about wind effects on survival or the breeding or wintering range distribution.

With no doubt, wind can have an important influence on migratory strategies. There are regions with stable wind conditions and regions with highly variable wind conditions, and winds show long-term shifts due to the global change. The study of bird migration and wind conditions enables us to investigate the evolution of reaction norms under natural conditions. However, the complexity of the environmental conditions necessitates straightforward hypotheses and large, long-term datasets.

Zusammenfassung

Vögel – Vom Winde verweht?

Die Zugvögel benötigen für ihre saisonalen Wanderungen zwischen Winterquartier und Brutgebiet ein gutes Orientierungssystem und ausreichend Energie um die z.T. gewaltigen Distanzen zu überwinden. Da sich der Zug selbst im Luftraum abspielt, der sich selbst ge-

genüber der Erde sehr variabel bewegen kann, kompliziert sich die auf den ersten Blick einfache Aufgabe erheblich. Einerseits gilt es seitliche Verdriftungen durch den Wind zu vermeiden oder zu kompensieren, um das vorgegebene Ziel zu erreichen. Andererseits ist die benötigte Energie für den Flug sehr stark von den Windbedingungen abhängig. Da der Aufbau von Energiereserven die Rastzeiten maßgeblich bestimmt, hat der Energieverbrauch im Flug einen bedeutenden Einfluss auf die Anzahl der benötigten Rastplätze und auf die Dauer des Zuges. Die normalen Windgeschwindigkeiten liegen in der gleichen Größenordnung wie die Eigengeschwindigkeiten der Vögel. Je nach Windsituation und Verhalten der Vögel, können die Flugkosten daher leicht verdoppelt oder halbiert werden. In zahlreichen Studien wurde untersucht in welchem Maße Zugvögel auf die herrschenden Windbedingungen reagieren, wie sie Verdriftungen kompensieren, Gegenwinde vermeiden und von Rückenwinden profitieren um ihre Ziele zu erreichen. Diese Arbeit fasst die verschiedenen theoretischen und empirischen Untersuchungen zusammen und versucht einen umfassenden Überblick zum Windeinfluss auf den Vogelzug zu geben. Unbestritten ist, dass die Mehrheit der Zugvögel für ihren Start zur nächsten Flugetappe starke Gegenwinde meidet. Einmal in der Luft, wählen sie ihre Flughöhe entsprechend den vorherrschenden Windbedingungen, d.h. sie suchen sich unter den gegebenen Bedingungen die relativ günstigsten Höhenbereiche aus. Für manche extreme Langstreckenflüge über Meere und Wüsten sind günstige Rückenwinde eine notwendige Voraussetzung für den erfolgreichen Zug. Die Kompensation von seitlicher Winddrift scheint zumindest bei einzelnen Arten altersabhängig, d.h. beeinflusst von ihrer Erfahrung. So lassen sich Jungvögel stärker vom Wind verdriften als Altvögel. Zudem weisen die unterschiedlichen Resultate zur Driftkompensation daraufhin, dass die Variabilität der Windbedingungen auf den verschiedenen Zugrouten die Reaktionsnormen der verschiedenen Arten und Populationen beeinflussen. Weiter wird diskutiert, welche Möglichkeiten die Vögel haben um Windbedingungen im Flug zu messen und wie anhand von Felddaten das Flugverhalten in Bezug zum Wind getestet werden sollte.

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