



In-flight reactions of nocturnally migrating birds to winds

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Abstract

Available knowledge on in-flight reactions of nocturnal bird migrants to winds is reviewed, with emphasis on the challenging topographical and meteorological conditions in Western Europe, and differences from the situation in North America discussed. Conclusions drawn are used for a new approach: using individual radar tracks of nocturnal migrants (mainly passerines) as well as winds measured at their flight altitudes, we defined the basic direction (BD = average flight direction of all migrants tracked under negligible wind influence) as a reference. For two altitudinal zones above a radar site near Nuremberg, we modelled the deviations of tracks and headings from BD for increasing wind from six 60° sectors. A comparison of birds' air speeds V_a with winds from four 90°-sectors confirmed that V_a increased with opposing winds from ~11 to 13 (14) m/s; a similar increase occurred with side winds. An expected, slight decrease of V_a with increasing following winds was only indicated for high-flying, not for low-flying birds. A predicted increase in average V_a due to decreasing air density with increasing height was not observed; possible explanations (birds climbing to high altitudes in following, but not in strong opposing winds) are discussed. Over the whole autumn migration season, headings were concentrated in a sector of $\pm 30^\circ$ around 230° in both altitudinal zones. Prevailing winds from 230 to 320° (SW–NW, i.e. opposing from right) led to widely scattered tracks primarily between 190° and 270° , but additional ones in the SE sector (mainly 100° – 170°). The analysis of tracks and headings relative to BD revealed the following features. (1) Overcompensation was frequently observed at low wind speeds (< 3 m/s); (2) under all wind conditions, but particularly with opposing winds and at low flight levels, tracks were widely scattered, including birds deviating more than 90° from BD. (3) Under opposing and side winds from the right compensatory efforts led to partial drift compensation up to wind speeds of ~8–10 m/s. Because efforts to compensate drift dwindled with increasing wind speeds, birds were fully drifted. Many even shifted their heading to due south and, hence, overdrifted. (4) Opposing and side winds from the left induced partial compensation at low flight levels and full drift above 1500 m asl. (5) The lateral components of the rare and weak following winds led to tracks close to expected minimal drift (without important compensation needed). In general, migrants compensated less for deviations by wind force than expected. The tendency of birds to maintain headings close to BD under opposing winds was so strong that many individuals continued migration with minimal progress over ground or even with retrograde migration as an extreme. On the other hand, there was an omnipresent fraction of birds with tracks far from seasonally favourable directions, including reverse migration.

Keywords Bird migration · Tracking radar · Basic direction · Drift · Compensation · Track · Heading · Flight altitude

Zusammenfassung

Reaktionen nachts ziehender Vögel auf aktuelle Windbedingungen

Vorhandene Publikationen über die Reaktionen nächtlich ziehender Vögel auf Windeinflüsse wurden – mit Fokus auf den herausfordernden topografischen und meteorologischen Bedingungen im westlichen Europa – zusammengefasst und Unterschiede zu den Verhältnissen in Nordamerika diskutiert. Daraus abgeleitete Folgerungen führten zu einem neuen

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methodischen Ansatz: Wir nutzten die individuellen Flugwege von Nachtziehern (mehrheitlich Singvögel) sowie auf der Flughöhe der Vögel gemessene Winddaten, um eine Basisrichtung (BD = mittlere Flugrichtung von bei vernachlässigbaren Windstärken ziehenden Vögeln) als Referenz zu definieren. Für zwei Höhenbereiche über einem Radarstandort in der Nähe von Nürnberg modellierten wir die Abweichungen der Flug- und Eigenrichtungen von BD für zunehmende Winde aus sechs 60°-Sektoren. – Ein Vergleich der Eigengeschwindigkeiten V_a mit Winden aus vier 90°-Sektoren bestätigte, dass V_a mit zunehmendem Gegenwind von ~ 11 auf 13 (oder gar 14) m/s zunahm; eine ähnliche Zunahme trat bei Seitenwinden auf. Zunehmende Rückenwinde induzierten dagegen keine eindeutige Reduktion von V_a . Eine aufgrund abnehmender Luftdichte erwartete Zunahme von V_a mit der Höhe konnte nicht festgestellt werden; wahrscheinlich, weil die Vögel bei starkem Gegenwind das Aufsteigen in den oberen Höhenbereich vermieden. – Über die ganze Herbstzugperiode waren die Eigenrichtungen in beiden Höhenbereichen konzentriert in einem Sektor von $\pm 30^\circ$ um 230° . Vorherrschende Winde von $230\text{--}320^\circ$ (SW-NW, d.h. Gegenwind von rechts) führten zu weit gestreuten Flugrichtungen vor allem zwischen 190° und 270° und zusätzlich Richtungen gegen den SE-Sektor ($100^\circ\text{--}170^\circ$). – Die Analyse von Flug- und Eigenrichtungen relativ zu BD deckte folgende Merkmale auf: (1) Überkompensation trat häufig auf bei geringen Windgeschwindigkeiten (< 3 m/s). (2) Unter allen Windbedingungen, aber speziell bei Gegenwinden auf geringen Flughöhen waren die Flugrichtungen weit gestreut und schlossen Vögel ein, die mehr als 90° von BD abwichen. (3) Bei Seiten- und Gegenwinden von rechts erzielten die Vögel Teilkompensation bis zu Windgeschwindigkeit von ~ 8–10 m/s. Abnehmende Kompensationsanstrengungen der Vögel mit zunehmender Windgeschwindigkeit führten zu vollständiger Verdriftung. Viele drehten ihre Körperachse gegen Süden und erreichten damit Über-Drift. (4) Seiten- und Gegenwinden von links führten zu Teilkompensation auf geringen Flughöhen und zu voller Drift oberhalb von 1500 m über Meer. (5) Die lateralen Komponenten der seltenen und schwachen Winden von hinten erlaubten Flugrichtungen nahe bei der erwarteten minimalen Drift, ohne wesentliche Kompensation. – Generell kompensierten die Vögel weniger für windbedingte Abweichungen als erwartet. Die Tendenz von Zugvögeln, die Ausrichtung ihrer Körperachse nahe bei BD zu halten, war so stark, dass viele Individuen ihren Zug fortsetzen, auch wenn sie bei starkem Gegenwind nur minim über Grund vorankamen oder als Extrem sogar vom Wind rückwärts getrieben wurden. Andererseits gab es einen beinahe ständig vorhandenen Anteil an Vögeln, die stark von saison-konformen Richtungen abwichen und dabei auch Umkehrzug zeigten.

Introduction and review

Migrating birds move with the body of air in which they fly. The movements of this medium have enormous effects on the time and energy budget of the migrants, and they may cause major problems for orientation (e.g., Shamoun-Baranes et al. 2017). The effects of strong adverse winds can be reduced by avoiding flights under such conditions. However, because westerly and south-westerly winds occur frequently in the western half of Europe, autumn migrants need to fly under such conditions to keep with their time schedule and, thus, are forced to implement means to cope with wind influence aloft (Erni et al. 2005). Once in flight, the birds can increase their air speed V_a or modify their heading R_a to mitigate deviations of their tracks R_g by wind. Counteracting adverse wind effects becomes increasingly demanding and essential for survival with increasing wind force. The vital importance of such behaviour has stimulated numerous studies in this field, particularly since radar facilitated the measurement of directions and speeds of nocturnally migrating birds. However, the circular distribution of winds and migratory movements implied major challenges for the analysis of available data. We will, therefore, provide a brief review of pertinent studies as a background for our own approach.

Our focus is on nocturnal migration in Western Europe, because topography and frequent unfavourable winds for

autumn migration require challenging adaptations. Limited considerations about the conditions in North America are included in the discussion.

Historical overview

Basic ideas about the influence of winds on migratory directions were provided by Alerstam (1976). He defined full wind drift (flying with a fixed heading), complete drift compensation (flying along a fixed track), and partial compensation (either compensating with respect to moving waves over water, or incomplete compensation of wind above land). The term “pseudo-drift” was used for wind-induced shifts in the observed mean flight directions (tracks) due to the supposed participation of different species or populations profiting from following winds to reach different intermediate goals. As a universal measure of drift, he suggested the linear regression coefficient b of track directions on α (the angle between track and heading directions). In a second part, he critically reviewed radar (mainly surveillance radar, thus not altitudinally differentiated) information on migratory movements and their relation to simultaneous wind situations (presented in publications from 1957 till 1975) and drew the following conclusions: (1) all the observed movements showed at least partial compensation for wind

drift; (2) ample evidence demonstrated the birds' capability for complete drift compensation, while most instances of observed drift appeared to be explainable by pseudo-drift; (3) some cases, however, indicated partial drift effects that could not completely be explained by pseudo-drift. Additionally, he stated that birds were extremely rarely overpowered by winds exceeding the birds' air speed. None of the studies suggested the existence of overcompensation (negative drift).

Besides immediate reactions to wind effects, Alerstam (1979a, b) suggested that birds might tolerate drift in the early phases of migration far from their goal by flying at high altitudes with relatively strong winds. Descending to lower flight levels with weaker winds towards the end of their flight would allow them to correct for previous drift. A different approach to estimate the influence of wind on track and heading directions was applied by Bruderer and Liechti (1990). They defined site-specific basic directions (BD) under minimal wind influence ($V_w < 5$ m/s) as reference directions to quantify wind-induced deviations from the bearing towards the assumed intermediate goals (along the BD). At Nuremberg in southern Germany, estimated BD for autumn migration was $\sim 230^\circ$ in the lowest 1000 m agl, and $\sim 218^\circ$ above, with only minor deviations due to different wing-beat classes or the progress of the season. In weak to moderate opposing winds from W, birds headed into the wind, but—apart from a slight increase in air speed—they did not augment their efforts to compensate for increasing wind force. Thus, drift increased with increasing wind speed. With very high wind speeds, the birds shifted their body axis southward. This was considered as tolerated southward or south-eastward drift, and not as pseudo-drift (see Liechti 1993 below).

Bruderer and Jenni (1990) found (based on the analysis of ringing recoveries of passerines crossing Switzerland and on birds caught in the Swiss Lowlands and on Alpine passes) that the mean recruiting directions shifted from 220 to 230° for short-distance migrants with low fat scores towards 200° for trans-Saharan migrants with high fat scores. Southerly directions and high fat stores suggested a provenience from northern populations and trans-Saharan migration, thus providing a plausible interpretation of the tracking radar data showing more southerly directions among high-flying birds.

Reviewing publications up to 1990, Richardson (1991) concluded that birds developed many adaptations to cope with wind effects: Particularly, high-flying birds may allow crosswinds to drift their tracks laterally from the preferred direction, while many low-flying birds compensate for drift, and may even overcompensate to make up for previous drift. Tolerating partial drift at high flight levels in the early stages of migration and overcompensating later by flying at low levels against weaker winds may even be considered an optimal strategy (Alerstam 1979a, b). Compensation may

be more common where there are prominent topographical features. Other adaptations include reduction of drift by flying at times and/or altitudes without strong crosswinds. The significance of pseudo-drift was put into perspective, but was still considered a major complication for the interpretation of field data.

Liechti (1993) analysed tracking radar data from the area of Nuremberg and showed that an increase in southerly tracks with altitude (in addition to the generally SW-oriented movements) was mainly due to winds. Under strong headwinds, the proportion of southerly headings increased and resulted in tracks towards SE or even E (at all heights). These SE movements were not considered as pseudo-drift, because SE flights were the result of drift with winds from W, but not downwind flights with NW winds. Partial compensation for wind drift by nocturnal migrants seemed to occur mainly in relation to wind direction rather than wind speed. Birds apparently adapted their drift compensation to relatively low wind speed at low flight levels. Thereby they were able to compensate completely for side wind speeds of less than 20% of their own air speed (i.e. about 2.4 m/s for small passerines); this means that average track directions remain $\pm$ constant under weak winds of all directions, but show increasing drift at higher wind speeds, resulting in diminishing partial compensation.

The relation between flight power and air speed of birds can be used to predict maximum range speed V_{mr} (Pennyquick 1972). This optimal air speed for minimizing cost of transport is modified by winds. Calculations of such modifications based on field data were based on head- and tailwind components (e.g. Bruderer 1971), while Liechti et al. (1994) demonstrated that side winds had an additional effect on V_{mr} . V_{mr} depends not only on the effect of wind on the bird's ground speed, but also on the bird's angle of compensation for side wind. Optimal air speeds should be faster in side winds than in pure tail- and headwinds. Critical tests of this prediction are, however, only possible if the goal direction is known and birds compensate completely for wind drift (i.e. only at very low wind speeds!).

A goal-oriented migrant optimizing energy expenditure during flight should adjust not only its heading, but also its air speed with respect to wind. Liechti (1995) introduced a model combining simultaneous modifications of headings and air speed in an optimal strategy (using a garden warbler *Sylvia borin* with a theoretical maximum range speed $V_{mr} = 10.5$ m/s as a model bird). According to this model, the angle of compensation culminates with side winds from behind ($\sim 60^\circ$), while adjustments in air speed are strongest with opposing winds. Increasing air speed under opposing winds results in a considerable reduction of drift.

Tracking-radar samples from the area of Lund led Bäckmann and Alerstam (2003) conclude that wind drift was the dominant cause of the large scatter of track directions,

especially during the autumn season. Besides drift, they detected partial drift compensation in spring, but not in autumn. In situations with low wind speeds, headings seemed to be slightly more concentrated in spring than in autumn, suggesting less accurate orientation in autumn, when a large proportion of the migrants are naïve juveniles. According to the presented data, we may also think of alternative interpretations: (1) birds are closer to their destination in spring and may—according to Alerstam (1979a,b)—correct for previous drift when approaching their goal areas; (2) considering that fast flying birds with wing-beat frequencies below 11.5 Hz were the dominating category of migrants, particularly in spring, and showed the highest concentration of heading directions, we may suggest that waders and waterfowl contributed to the reduction of drift in spring.

Liechti (2006) summarized studies on flight behaviour of migratory birds in relation to winds published during the 15 years since Richardson's (1991) review. These studies corroborate that birds select favourable wind conditions for departure as well as aloft to save energy. For some long-distance migrants, tailwind may even be an indispensable support to cross large barriers. A new aspect was brought into discussion by proposing a simple method for drift detection by the migrants: A flying bird may determine the angle between its body axis (heading) and flight direction (track) by observing the angular velocity of landmarks to the left and right below its flight path. Maximum angular velocity is always right-angled to the flight direction (irrespective of heading). Without lateral drift, the maximum angular velocity of landmarks occurs also at right angles to both sides of the body axis. With increasing drift, maximum angular velocities deviate increasingly from the body axis: on the lee (downwind) side, landmarks in front of the bird move faster, while on the windward side, the landmarks on a diagonal behind the bird move faster. Obviously, the effectiveness of such a procedure decreases with increasing height above ground. Compensation for lateral wind drift reduces the risk that the flight routes would mainly 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 wind or at least avoid costly wind effects.

Green and Alerstam (2002) evaluated four methods that had been used to quantitatively estimate wind drift or compensation. They found that the original method of Alerstam (1976) provided robust and reliable results. In contrast, regressions of individual flight directions in relation to α (in this case, the angle between track and heading for individually tracked targets) proved to produce biased and spurious results, overestimating compensation under following winds, while overestimating drift under opposing winds. The authors state that “comparing mean directions for cases with winds from the left and right in relation to

individual flight directions also gives biased and spurious results unless there is full variation in wind directions or an equal distribution of crosswinds from left and right”. As an alternative, we suggest considering the influence of winds from different sectors separately.

A general background to the present study is given by the publications of Bruderer & Peter (2022) on the directions of autumn migration between Europe and the West African savannas and Bruderer et al. (2018) on the vertical distribution of bird migration between the Baltic Sea and the Sahara.

Aim

Instead of analysing the problem of drift vs compensation for entire migratory movements (as suggested by Thomas Alerstam and colleagues), we wanted to know how individual nocturnal migrants react to winds of varying speeds and incident angles. To avoid the problems arising due to the circular distribution of winds and migratory directions (mentioned by Green and Alerstam 2002), we analysed the reactions of birds to winds from different sectors. The incident angles were measured relative to a site-specific basic direction (BD), where BD is the average travel direction of birds migrating under negligible wind influence through a given area in a migratory season.

Nocturnal migrants (mainly passerines) tend to engage in migration when their position relative to cyclones and anticyclones is optimal (Richardson 1990), usually when winds follow and the probability for rain is low (Erni et al. 2002). Once airborne, the birds move with the air mass in which they fly. This “physical drift” (passive displacement by wind) reduces a bird's progress with respect to its intermediate or final goal; thus, it would be meaningful for the bird to either land or optimize its flight behaviour to mitigate negative effects, e.g. by choosing flight altitudes with less unfavourable wind, or by adjusting its air speed and/or heading. The wind vector and the bird's own movement together result in the track of the bird. We used the difference between physical drift (i.e. zero compensation) and the average track directions of the birds per wind sector to quantify the effectiveness of the migrants to mitigate the effects of wind. The reactions of the birds were visualized by comparing the theoretical heading required for full compensation under increasing wind force with the averages of measured headings in each sector.

The ideas on wind-dependent reactions of migrating birds presented in the reviewed publications lead us to the following hypotheses:

(H1) Air speeds of birds increase with opposing and side winds, and slightly decrease in following winds.

- As suggested by Pennycuik (1972) by the curve of power versus speed, predicting that the speed of maximum range V_{mr} (minimising energy cost per unit distance travelled) increases with opposing winds and decreases with following winds.

(H2) Air speeds of birds increase with altitude.

- This according to flight aerodynamic theory predicting that air speed increases with decreasing air density.

(H3) Opposing and side winds (relative to BD) are fully compensated at low wind speeds, while higher wind speeds lead to increasing drift.

- Testing Liechti's (1993) conclusion that average track directions remain $\pm$ constant under weak winds from all directions, but show increasing drift at higher wind speeds.

(H4) High wind speeds (close to or exceeding the birds' air speed) lead to full drift or even overdrift.

- Verifying the observation of Bruderer and Liechti (1990) that besides drift increasing with wind speed, birds seemed to shift their body axis southward at very high wind speeds, thus augmenting southward or south-eastward drift.

(H5) Winds from the right (in autumn from W and NW) favour more drift than side winds from the left (in autumn S).

- Because in Western Europe southward drift (by winds from W and NW) brings autumn migrants closer to their southern destinations than drift towards the right (NW).

(H6) Reverse migration occurs in most nights, but is favoured by winds opposite to preferred migratory directions (which are towards SW in autumn).

- Re-considering a statement of Komenda-Zehnder et al. (2002) that a small proportion of reverse migration is an intrinsic feature of nocturnal bird migration, and its volume is not explainable by weather factors (in the trade-wind zone of Israel).

(H7) Retrograde migration (birds flying backwards, i.e. tail-on with the wind) can be observed under opposing winds surmounting the birds' flight capacities.

- Richardson (1991) mentioned the occurrence of "retrograde migration" of birds being blown backwards by headwinds exceeding their air speed.

(H8) Downwind flights towards SE (towards south-eastern goal areas and thus pseudo-drift) are rare.

- Pseudo-drift (due to varying proportions of birds with differing goal areas) is often mentioned, but is suggested to be rare in southern Germany by Liechti (1993).

(H9) Following winds do not require much compensation due to concentrating wind effects. Within the expected narrow range, we expect similar reactions as suggested under points 3 and 4.

- Despite minimal requirement of compensation, residual reactions are expected.

In the results, we refer to these hypotheses by the number of the hypothesis (H_x) and an indication whether the results agree fully (H+), partially (H $\pm$), or not at all (H-) with the corresponding hypothesis.

Methods

The present study is based on the data of a complete autumn season at Lehrberg near Nuremberg (10° 31' E/49° 29' N, 450 m asl, 30 July–30 Oct 1987). This allowed us to analyse the flight behaviour of nocturnal migrants above a landscape without pronounced topographical features. Continuously flapping birds made up only 6.4% of all tracked birds. Thus, the results reflect mainly the behaviour of intermittently flapping passerines.

The tracking radar "Superfledermaus" was used to track migrating birds and pilot balloons (to measure wind vectors) over the last 50 years; technical improvements comprised mainly recording techniques and signal processing (Bruderer 1971, 2020; Bloch et al. 1981; Bruderer et al. 2012). Since 1991, the polar coordinates of the tracked objects (birds or pilot balloons) provided by the radar at intervals of 1 s were digitized, transformed into Cartesian coordinates, and averaged over 20 s. These averages were used to calculate the mean flight direction (track), heading, height above radar, ground speed, and air speed as well as vertical speed per individual.

For detailed studies, birds tracked between 20 and 05 h were included in the standard analysis (provided their air speed V_a was > 5 and < 25 m/s, and their vertical speed V_z > -5 and < 3 m/s; thus excluding a few unrealistic extremes). Whenever possible, the wind measurement at midnight (with the best preconditions for undisturbed

laminar air currents and least time difference to the individual bird tracks) was used for the calculation of headings and air speeds of all night migrants. In the rare cases when this measurement was lacking, the wind data of the nearest evening or morning pilot balloon was used. For altitudinal comparisons, we defined two altitudinal zones below and above 1500 m asl (corresponding to < 1000 and > 1000 m

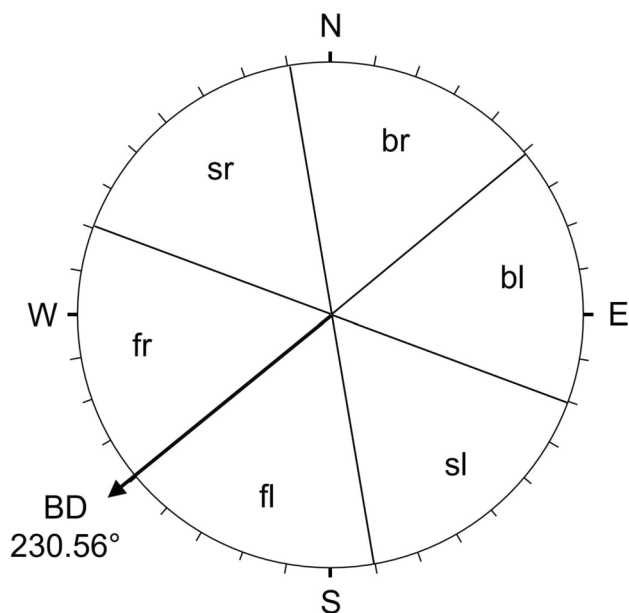


Fig. 1 Six wind sectors of 60° each, arranged to both sides of the basic direction BD (= 230.56° below 1500 m asl). The sectors represent opposing, following, and side winds from left and right, respectively

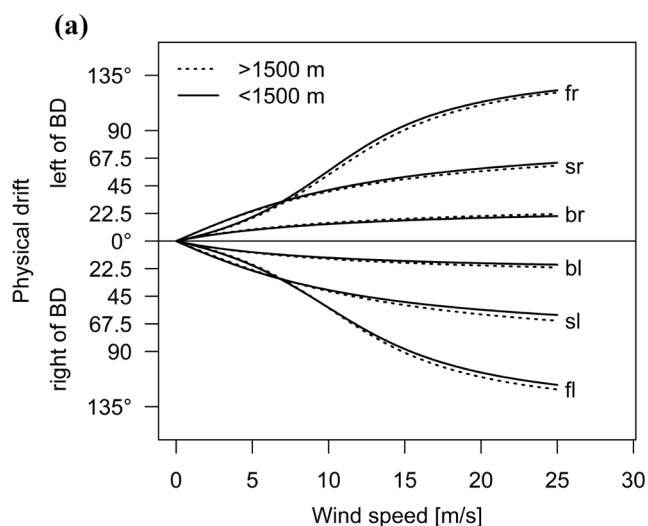


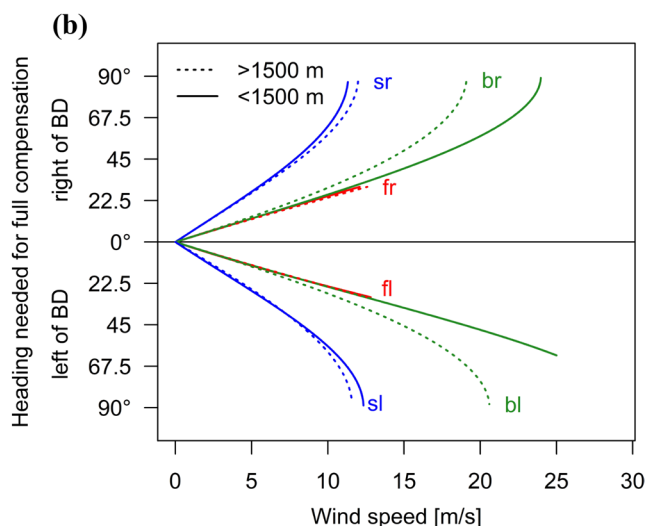
Fig. 2 a Resulting physical drift with increasing wind speed from six sectors (according to Fig. 1), with full lines for the lower and dotted lines for the upper altitudinal zone (< 1500 m and > 1500 m asl,

agl in the relatively flat area roughly 500 m asl, aiming at comparable numbers of tracked birds per height bin).

We defined the basic direction (BD) as the mean direction of the tracks recorded in the considered area under minimal wind influence, over the entire observation period (Bruderer and Liechti 1990). As BD may differ between altitudes, we calculated it for the two altitudinal zones, using the track directions of all individuals flying in weak following winds ($V_w < 5$ m/s) or in even weaker opposing and side winds ($V_w < 3$ m/s). The resulting BD was 230.56° below 1500 m asl, and 216.54° in the upper height bin. We bear in mind that BD is a convention that includes considerable uncertainty due to individual variation of migratory directions, thus calculating decimals is a matter of mathematics, not of biology.

We assigned wind directions to six sectors (wind categories, Fig. 1) and analysed the deviations of tracks and headings from BD per wind sector. The track directions represent vector additions of a bird's own movement and the wind vector. To visualize the difference between passive transport and the birds' own efforts, we calculated curves of physical drift with increasing wind speed for each wind sector. Physical drift is the deviation of a bird that flies with an average air speed exactly in the basic direction under the wind direction in the centre of the sector in question with a speed that can be read from the Y-axis (Fig. 2a).

The deviations of the bird's headings from BD show (within the defined wind sectors) the reactions of the birds to increasing wind speed. The headings needed to fully compensate the actual winds from six different sectors provide a basis for the comparison of the birds' reactions with perfect compensation (Fig. 2b).



respectively) **b** Average headings needed to fully compensate drift with increasing speed of winds from six sectors (according to Fig. 1). Full lines for altitudes below and dotted lines above 1500 m asl

We compared the physical drift with the observed drift in relation to wind speed. We also compared the deviations of the birds' headings (bearing of the body axis) from BD with increasing wind speed, to show the reactions of the birds to winds. The mean of heading is compared with the line showing full compensation. To estimate mean drift and mean heading, we fitted robust general additive models per wind sector and flight level (using a Student-*t* data distribution; separate models for drift and heading), modelling a smoothed effect of wind speed and including a temporal autocorrelation. The model was fitted by the functions *brm* (package *brms*, Bürkner 2017; 24000 draws retained after warmup) and *s* (for the smoothing; package *mgcv*, Wood 2017; using the default for the degree of smoothing). For the tracks, we also present the medians of raw data per 1.5 m/s increase of wind speed.

Terms, definitions, and abbreviations:

V_a = air speed (speed relative to the surrounding air).

R_a = heading = bearing = direction of the body axis.

V_w = wind speed (speed of moving air masses).

R_w = wind direction (provenience of moving air masses).

V_g = ground speed (speed relative to the ground).

R_g = track = direction or flight path over ground = vector addition of $R_a + R_w$ (arrow above for vector) V_{mr} = air speed V_a allowing a bird to cover the maximum range by minimizing the energy cost per unit distance travelled.

Basic direction = BD = average track direction of the migrants flying under negligible wind influence.

Overcompensation = birds shift their body axis more than expected for full compensation of the actual side wind components (leading to negative drift).

Overdrift occurs when compensation is negative, resulting in tracks being deflected more than expected by physical drift.

Recruiting direction = direction where the migrants come from.

Retrograde migration = birds are blown backwards by strong opposing winds.

Reverse migration = migration opposite to the directions expected for the season.

Physical drift = displacement of an airborne object (like a balloon) with the moving air = full drift.

Pseudo-drift = changes in the spectrum of migratory directions due to differential use of following winds by populations or species with different intermediate goals.

Wind drift = drift = resulting movement of a bird, based on physical drift and the reaction of the bird.

Sectors denoting the origin of winds relative to BD: fr, fl = front-right, front-left, sr, sl = side-right, side-left, br, bl = back-right, back-left.

Wind directions relative to the birds: side winds from right and left (sr, sl), opposing (fr, fl), following (br, bl).

agl = above ground level; asl = above sea level.

Two altitudinal zones (above or below ~1500 m asl) = height bins (above or below ~1000 m agl) = flight levels.

Results

Directional distribution of tracks, headings, and winds

We may assume that the recorded headings provide an approximate indication of (rather short-range) intermediate goal areas of the migrants, while the tracks include the influence of winds and the reactions of the birds. Figures 3a–d provide a general overview of the available winds and those used by the migrants, leading to first conclusions about selective behaviour of the birds.

While *tracks* were widely scattered between 100° and 310° (i.e. from ESE to NW) at low flight levels and 110°–270° higher up, headings were concentrated around the basic direction BD, mainly between 200° and 260° in the lower altitudinal zone, and slightly more S at the upper level (roughly 200°–260°). The concentrated headings contrasting with the scattered tracks reveal important wind drift (Fig. 3a).

The diagram of the available and used wind directions (Fig. 3b) shows that most birds had to fly with opposing winds from the right of their body axis. Winds were used according to availability, except an overproportional use of SE winds and a concentration of high-flying birds in the central part (260°–290°) of the available wind directions. Winds from *E* and particularly *W* were on average stronger than those from *S* and particularly *N*, but the average wind speed was astonishingly low, i.e. <5.3 m/s.

The directional distribution of available and used wind speeds (Fig. 3c) reveals that the low-flying migrants avoided the strongest opposing winds from the right of BD (fr, ~230°–270°), while preferring strong following winds from the left (bl, ~50°–100°). A consequence of head-wind avoidance was that opposing side winds from WNW (280°–330°) and from SW (200°–220°) got more relative importance than the strongest and most frequent (but avoided) winds from sector WSW in our data set. In the upper height bin, the available winds from the *W* (230°–330°) were stronger than in the lower bin, as expected according to wind pattern in the lower troposphere. Wind speeds from due *W* averaged over the whole season reached 13.24 m/s. The averaged used wind speeds towards this directions were, however, only 4.9 m/s. This indicates a pronounced selectivity for low wind speeds under opposing winds (at both flight levels).

For a better understanding of the directional and altitudinal distribution of the tracked individuals, Fig. 3d shows

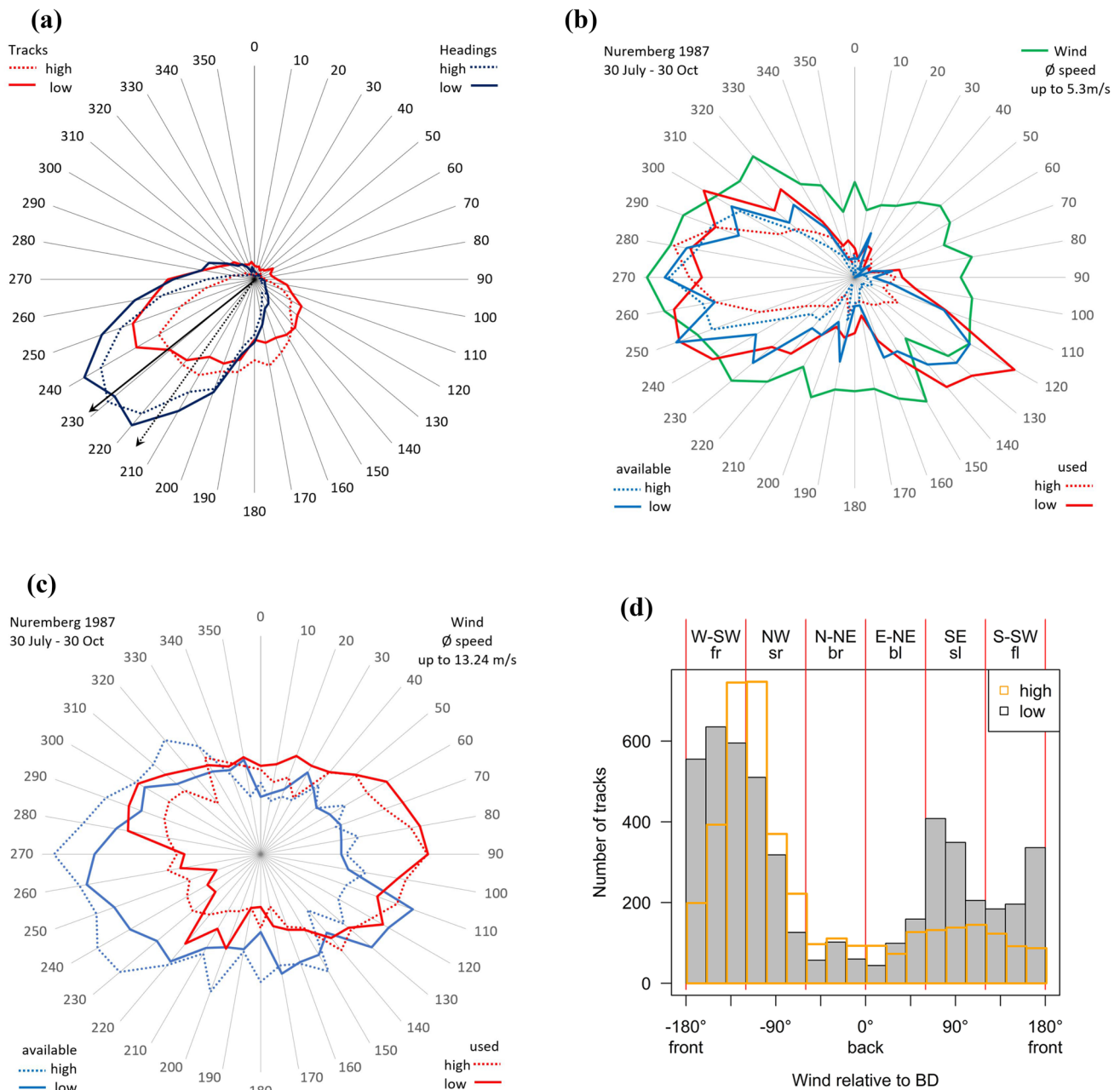


Fig. 3 **a** Proportional distribution of tracks (red) and headings (blue) of nocturnal migrants tracked during autumn 1987 (1 August – 30 October 1987) near Nuremberg. Black arrows = BD. Full lines below 1500 m asl, and dotted lines above 1500 m asl. **b** Distribution of wind directions (directions of origin) during autumn 1987 near Nuremberg. Available winds (blue) and winds used by the tracked birds (red). Full lines below 1500 m asl, and dotted lines above 1500 m asl, both scaled to the same maximal value. The average wind speed per direction is shown in green (scaled to reach the highest value at

270° with 5.3 m/s). **c** Average wind speed per 10° class of wind directions (direction of origin). Available winds (blue), and winds used by the tracked birds (red). Full lines below 1500 m asl, and dotted lines above 1500 m asl. Scaled as in **b**. **d** Distribution of wind directions used by the tracked birds flying above (yellow) and below (black) 1500 m asl. Histogram bins chosen to reflect our classification of winds into wind sectors relative to BD, with three classes per sector to visualize gradual changes in the distribution of high- and low-flying birds (color figure online)

the number of recorded flightpaths for each third of a sector: according to the distribution of available winds, most birds flew in the sector with winds from W–SW (fr), most of them in the lower altitudinal zone, but with increasing proportions

of highfliers towards the right of the sector. The increasing proportion of high-flying birds continued into the sector NW (sr) and persisted throughout this sector as well as in sector br (with rare winds from N–NE). Across the sectors sl and

fl, the proportion of high flights was relatively small. Within the sector fr, the proportion of high flights increased; this prevailing of high flights continued across the sectors sr, br, and partially bl. While the general distribution of tracks was due to the availability of winds, the altitudinal distribution may indicate that more birds were prepared to climb to the upper flight level with wind components from the right and from behind.

Prospects and limits of drift compensation

To get an idea of the range and intensity of the birds' reactions to winds, Fig. 4 exemplifies theoretically (based on flight-path recordings and associated winds from three sectors to the right of BD up to an altitude of 1500 m asl) the course of three flight parameters with increasing wind speed and full compensation (black line: R_a ; purple line: mean V_a ; orange line: resulting ground speed V_g).

The left graph in Fig. 4 shows that winds from front-right (fr) increasing from 0 to 25 m/s could be compensated completely by shifting headings (R_a , black line) continuously from 0° to about 30°, the resulting ground speed dropping to zero at $V_W = 12$ m/s. The air speed V_a (purple line) increased from 11 m/s to roughly 14 m/s with wind speed increasing from 0 to 25 m/s (corroborating Pennycuick's 1972 prediction about maximum range speed V_{mr} , H1 +), while the resulting ground speed V_g (orange line) decreased linearly from 11 to 0 m/s.

Middle graph (with same colour code as left graph): With side winds from the right (sr), V_a increased from 10.5 to about 12.5 m/s for an increase of V_W from 0 to 25 m/s (H1 +). Headings needed for full compensation increased

towards 90°; ground speed declining steeply towards 0 at $V_W = 11.5$ m/s.

Right graph: With following winds from the right (br), headings for full compensation approached 90° at wind speeds close to 24 m/s, while ground speed increased up to $V_W = 24$ m/s, then decreased to about $V_W = 22$ m/s. V_a increased only slightly from 11 to 12 m/s (H1 ±).

Variation of air speed with wind speed

One option of a bird to compensate for wind effects is by increasing air speed (V_a)—as suggested by the purple line in Fig. 4.

Figure 5 visualizes the variation of mean air speeds with increasing wind force (V_W) from four sectors of incident wind (opposing, following, and side winds from left and right) at two flight levels. According to Fig. 5, mean air speeds showed increasing trends with increasing speed of opposing and side winds in both altitudinal zones (H1 +) as expected according to Pennycuick's (1972) model on the influence of wind on maximum range speed V_{mr} . The highest average V_a reached about 13 m/s under high wind speeds. An expected slight decrease of V_a with increasing following winds was only indicated for high-flying, not for low-flying birds (H1 ±). Under weak winds ($V_W < 3$ m/s), the all-over average of V_a from both altitudinal zones was ~11 m/s. Under these weak winds, V_a was marginally higher with opposing winds than with other wind directions. The average increase of V_a per step of 3 m/s increase of opposing winds varied around 0.4 m/s, indicating that the birds compensated roughly 10–20% of weak to moderate opposing winds. An unexpected lack of higher air speeds at high compared to low flight levels (H2 ±) will be commented in the discussion.

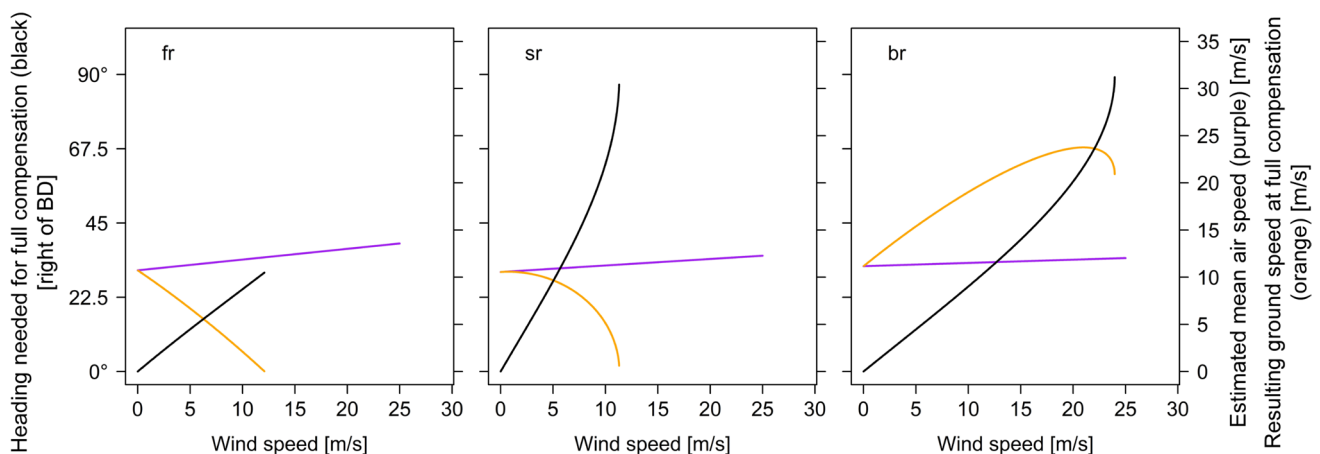


Fig. 4 Prospects and limits of drift compensation with increasing wind speed for three wind sectors from the right according to data from the radar site near Nuremberg at flight levels below 1500 m asl: resulting ground speed (orange line) when a bird fully compensates

wind drift, headings needed for full wind compensation (black, same line as given in Fig. 2b), and the mean air speed estimated from the data per wind sector (purple) (color figure online)

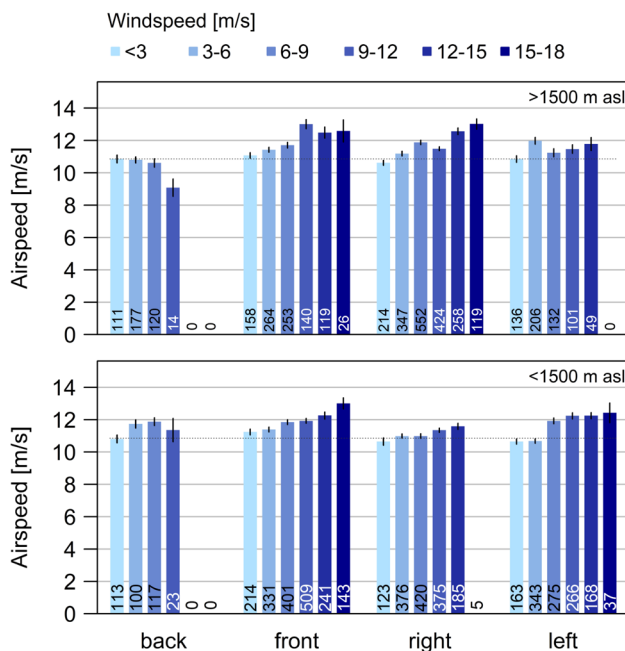


Fig. 5 Mean air speeds V_a (with standard error) of migrants flying in two altitudinal zones with winds from four sectors, arranged according to six wind speed classes. The dotted line indicates average V_a with least wind influence. Numbers within each column indicate sample size

Track directions and headings under varying winds

This chapter comprises the principal results of our study. To get the message, it is necessary to have the corresponding graphs of Figs. 6 and 7 at hand. For two height bins (low and high) and three pairs of left and right wind sectors (front fl, fr; side sl, sr; back bl, br), these figures visualize the deviations of track and heading directions from BD with increasing wind speed (Fig. 6). Figure 7 shows the circular distributions of tracks and headings per wind sector and altitudinal zone.

Each of the following paragraphs describes the directional reactions of birds to increasing wind speed within a sector of wind direction (according to Fig. 1), first in the lower height bin, and then for the higher flying birds. The graphs in the left column show the tracks, and those in the right column the headings. The raw data (small circles in each graph) show the full scatter of directions as well as the distribution of the recorded birds along the wind axis. Green lines in the left graphs indicate full drift for a bird flying with average speed and zero compensation, and green lines in the right graphs represent headings needed for full compensation (given average flight speed). Violet regression lines (with dotted lines indicating 95% uncertainty intervals) visualize estimated mean deviations of tracks and headings from BD (i.e. average drift and compensation, respectively). Blue circles (with a diameter

according to sample size) are medians of the tracks per 1.5 m/s increase of wind speed.

The distribution of raw data (red circles) shows that most tracked birds had to deal with wind speeds in the range of 2–14 m/s. Headings show astonishingly small mean deviations from BD. Accordingly, mean estimated tracks often follow rather closely the lines of full drift. Opposing winds from front-left (fl) low: winds from this sector were rather rare according to Fig. 3b. The regression line of widely scattered headings suggests compensation of weak winds (<3 m/s). Lacking increase of compensatory efforts with increasing wind speed led to increasing drift (H3+). However, wide scatter of tracks (red circles of raw data) towards left pulls the regression line and the medians away from the green line of full compensation up to wind speeds of 12 m/s. Reverse migration was prominent (H6+). Birds flying against headwinds stronger than their maximum air speed prove the occurrence of retrograde migration (H7+).

Opposing winds from front-left (fl) high: headings and tracks at low wind speeds indicate compensation or overcompensation, shifting towards full drift at higher wind speeds (H3+). Retrograde migration occurred in low numbers also at high altitudes (H7+).

Opposing winds from front-right (fr) low (the most frequent winds): headings indicate compensation or overcompensation with $V_w < 3$ m/s (H3+); tracks suggest negative drift up to $V_w = 6$ m/s. With increasing wind speed, headings shifted towards no and even negative compensation (H3+); tracks resulted in overdrift particularly with $V_w = 8$ –16 m/s (H4+, H5+). Above $V_w \sim 18$ m/s this overdrift disappeared, but did not reflect adequately the negative compensation shown by the headings. Reverse migration was massive under the given conditions (H6+), quite some headings indicating downwind flights.

Opposing winds from front-right (fr) high: the regression line of headings suggests compensation or overcompensation with wind speeds $V_w < 3$ m/s, tracks indicating negative drift up to $V_w \sim 7$ m/s). At wind speeds above 3 m/s, compensation diminished towards zero, while tracks approached full drift (H3+), minimal overdrift indicated by the medians under wind speeds of 12–14 m/s (H4+, H5+).

Side winds from left (sl) low: headings indicate slight overcompensation at lowest wind speeds, going over to partial compensation and insufficient increase with wind speed, tracks indicating partial drift up to $V_w \sim 15$ m/s (H3±); few tracks above this limit may suggest overdrift (H4+, H5–).

Side winds from left (sl) high: headings indicate slight compensation at lowest wind speeds, shifting to zero compensation above $V_w \sim 4$ m/s (H3+); tracks show full drift up to $V_w = 11$ m/s (H4+) and possible overdrift above (contradicting H5 as in the lower height bin).

Side winds from right (sr) low: headings indicate overcompensation at very low wind speeds, resulting in negative

drift in the tracks. Weak compensation remained nearly constant with increasing wind speed, thus leading to partial drift up to $V_W \sim 8$ m/s, shifting towards full drift and even overdrift above (H3 +, H4 +). The graphs do not indicate more drift with winds from the right than from the left (H5–).

Side winds from right (sr) high: headings indicate overcompensation leading to negative drift in the tracks at low wind speeds. With higher wind speeds, the regression lines of headings and tracks shift towards partial compensation/drift up to $V_W \sim 9$ m/s. Above this wind speed compensatory efforts decreased, and tracks shifted to overdrift (H3 +, H4 +, H5 +). The exceptionally high number of tracks in the upper height bin is explained by Fig. 3d.

Following winds from back-left (bl) low: headings and tracks indicate compensation or overcompensation up to $V_W \sim 3$ m/s. Compensation efforts did not increase sufficiently with increasing wind speed; thus, tracks approached full drift with wind speeds $V_W = 5–9$ m/s (H9 +, H3 +), and slight overdrift above (H4 +, H5 ±).

Following winds from back-left (bl) high: overcompensation in headings at low wind speeds ($V_W < 3$ m/s) led to negative drift in the tracks. Headings indicate negative compensation at higher wind speeds, thus leading to overdrift in the tracks (H9 + = H3 +, H4 +, H5–).

Following winds from back-right (br) low: a few scattered headings and tracks may indicate slight overdrift below $V_W \sim 2$ m/s, overcompensation between $V_W = 2–5$ m/s, and partial drift above (H9 +, H5–).

Following winds from back-right (br) high: few data suggest (southward) overdrift in tracks and headings below $V_W = 2$ m/s, partial compensation between $V_W = 2–5$ m/s, and overdrift above (H9 +, H5 +).

The flight behaviour of birds in the area of Nuremberg provided (in both altitudinal zones) at least partial support for most of the hypotheses put forward in the introduction (except H5, with ambiguous results) and H2, which is astonishingly not supported (see discussion). Directional deviations are similar at low and high altitudes, tendentially with reduced compensation higher up.

Figure 7 visualizes the results of Fig. 6 in circular diagrams, and thus a presentation closer to our spatial perception. These diagrams allow a general comparison of the directional distributions between the two altitudinal zones and the six wind sectors (which slightly differ between the zones according to differing BD): the directional distributions of the headings differed less between the height bins than the calculated BD. Headings showed the strongest compensation under side winds from the right (sr), the resulting tracks scattered around SSW at low levels and SSE higher up; birds were thus somewhat more efficient when closer to the ground. Compensatory efforts were less pronounced or even comprised overdrift with opposing winds from the right

(fr), leading to pronounced shifts of most tracks towards SE, particularly at low levels (H5 +). Low wind speeds in the sector with side winds from left (sl) induced moderate drift with little scatter. Following winds (bl and br) were associated with increased scatter of headings and weak signs of drift.

Conclusions and discussion

This re-analysis of the radar tracks of migrants from Nuremberg confirm and refine earlier analyses by Liechti (1993). The general finding is that in a relatively flat area of southern Germany, full compensation or overcompensation was the prevailing reaction of nocturnal bird migrants to deviating winds with speeds of less than 3 m/s. Under stronger winds, the radar-tracked birds showed insufficient or even decreasing compensation, so that drift became the predominant feature of migration under moderate to strong winds. Southward overdrift was conspicuous under the frequent winds from front-right. Despite some omnipresent reverse migration, we found no support for the idea that songbird migrants tend to fly downwind irrespective of wind direction as suggested, e.g. by Gauthreaux and Able (1970) for North America. We assume that reactions to winds are similar on both continents, but the frequently available northerly winds may allow autumn migrants in the northern USA (north of about 35° N) more drift tolerance than the birds in Central Europe that are confronted with predominant westerly winds (Fig. 3b). Some North American studies are reconsidered below.

Methodological limits

Tracking pilot balloons to get information on wind conditions at the flight altitudes of individually tracked birds is the most exact method to study the reactions of individual nocturnal migrants to winds. Nevertheless, temporal differences of up to several hours and ± 100 m in altitude between wind measurements and bird tracks induce some uncertainties. A mixture of species in our samples is an additional source of scatter. Fortunately, earlier studies showed that only about 6–7% of the tracked birds in Central Europe consist of continuously flapping birds, considered as waders or waterfowl (Bruderer 1971; Liechti 1993). The proportion of swifts was only relevant in the first half of August (with about 20%), then declined rapidly. Most of the birds were intermittently flapping passerines (averaged over the whole season 93.6%, with 71% small and 22.6% large passerines), the relative importance of large passerines increasing in October (Liechti 1993). This mixture implies some variation, because birds with higher flight speeds (e.g. waders vs. passerines or large vs. small passerines) have a higher



Fig. 6 Deviation of track directions (left graphs) and of headings (right graphs) from BD plotted versus wind speed. For opposing winds (front-left and front-right, first page 6a), side winds (side-left and side-right, second page 6b), and following winds (back-left and back-right, third page 6c). Twin graphs for the two altitudinal zones (low and high) directly above each other. The distribution of raw data is shown in each graph by small red circles. Green lines in the left graphs indicate full drift for a bird flying with average speed and zero compensation, green lines in the right graphs represent headings needed for full compensation (given average flight speed). Violet regression lines (with dotted lines indicating 95% uncertainty intervals) visualize estimated mean deviations of tracks and headings from BD (i.e., average drift and compensation, respectively). Tracks outside the grey lines at 90° show birds that make no progress with respect to an intermediate goal (along BD); birds with more than 150° deviation indicated as small grey circles. Shaded areas between $V_W = 11$ and 14 m/s indicate the range in which the birds can increase their air speed to mitigate adverse effects of opposing winds. The scale of the X-axis is adjusted to available wind speeds. Total sample size is indicated in the lower right corner of the heading graph (number of grey circles in brackets). The medians of tracks per 1.5 m/s increase of wind speed are indicated by blue circles (sample sizes per smallest and largest circle indicated to the right in the graphs of tracks)

capacity for drift compensation; small passerines, on the other hand, have wider power margins to adjust their air speed, and thus more flexibility to counteract drift within their lower capacity (Pennycuik 1972; Bloch et al. 1981). In the Alps, we found indications of increased propensity of (particularly small) waders to leave the inhospitable area in opposing winds by reverse migration, possibly returning to more suitable habitats in the lowlands (Bloch et al. 1981). Overall, we must contend with the fact that the scatter in our samples is increased by a mixture of species and populations with potentially diverging behaviour. To maintain awareness of this astonishingly broad variation, we present the raw data in our analyses of the migrants' reactions to winds in Fig. 6. The standard deviations of headings are usually in the range of $\pm 30^\circ$, the scatter of tracks considerably extended under opposing winds. Additionally, most distributions comprised some birds heading in seasonally inappropriate directions (deviating more than 90° from BD).

An important feature of our approach is the definition of the basic direction BD as an estimate of the intermediate goal area of the average migrants. Average track directions under “negligible” wind influence were considered as a valid reference for the comparison of wind-dependent deviations, allowing more general use than other reference directions, such as local leading lines (Åkesson 1993; Sinelschikova et al. 2020) or the direction towards a large intermediate goal area (McLaren et al. 2012). Baumgartner and Bruderer (1985) used the spectrum of directions derived from lines between ringing and recovery sites crossing defined areas to compare these with the directions observed on various surveillance radars. However, the selection of species was an arbitrary procedure, particularly with respect to the SW and

SE flyways. As most of the birds were recovered in the SE part of the Iberian Peninsula and southern France, the shift of directions around the western part of the Alps was more or less neglected by this method with the result that the average direction roughly corresponded to the BD of high-flying birds over Nuremberg. Frequently observed overcompensation under minimal wind speeds reduces the concentration of track directions around BD, but does not seem to induce notable shift in average directions, because overcompensation occurred to both sides. In the upper altitudinal zone, our calculated BD may be slightly too far S, because in Fig. 3a the headings of high-flying birds are only slightly shifted southward at the northern edge of the distribution. Liechti (1993) calculated BD values between 220° and 225° for high-flying birds. Despite this uncertainty, we maintained our calculated 216° , because the headings of high-flying birds in Fig. 6 showed no obvious deviation towards the right of the accepted BD.

Richardson (1990) concluded in his updated review that (according to many radar studies) numbers of migrants aloft are strongly correlated with following or light winds. Bruderer (1971) provided one of the early studies quantifying such relationship. Bruderer et al. (1995) and Liechti et al. (2000) showed (by counting the birds crossing the radar beam at various elevation angles) that nocturnal migrants even selected flight altitudes with best wind support. The present data seem to contradict such observations because the largest numbers of tracks had been recorded under opposing winds with moderate to high speeds (mainly between 4 and 12 m/s). This discrepancy is due to the use of two different methods: a) quantifying the passage of birds (in the earlier studies) and b) tracking birds with the aim to obtain comparable numbers of birds per unit time and altitude (in the present study). Tracking data reflect primarily the occurrence of winds, not the number of birds aloft.

Results put into perspective

A large set of tracking radar data covering a full autumn season in a relatively flat area in southern Germany served as the main basis for a study by Liechti (1993) and was used for comparisons with other radar sites by Bruderer and Liechti (1990). These papers provide valuable illustrations of recorded flight directions and their variation according to progress of season, wing-beat classes, altitude, and wind conditions, some also with geographical location. The present study analyses the influence of increasing speed of winds from particular sectors, and thus refines earlier results, but also confirms existing conclusions. (A) Liechti's (1993) statement that birds compensate only completely for side wind components reaching about 20% of their own air speed is confirmed and complemented by our observation of full compensation and overcompensation up to $V_W \sim 3$ m/s,

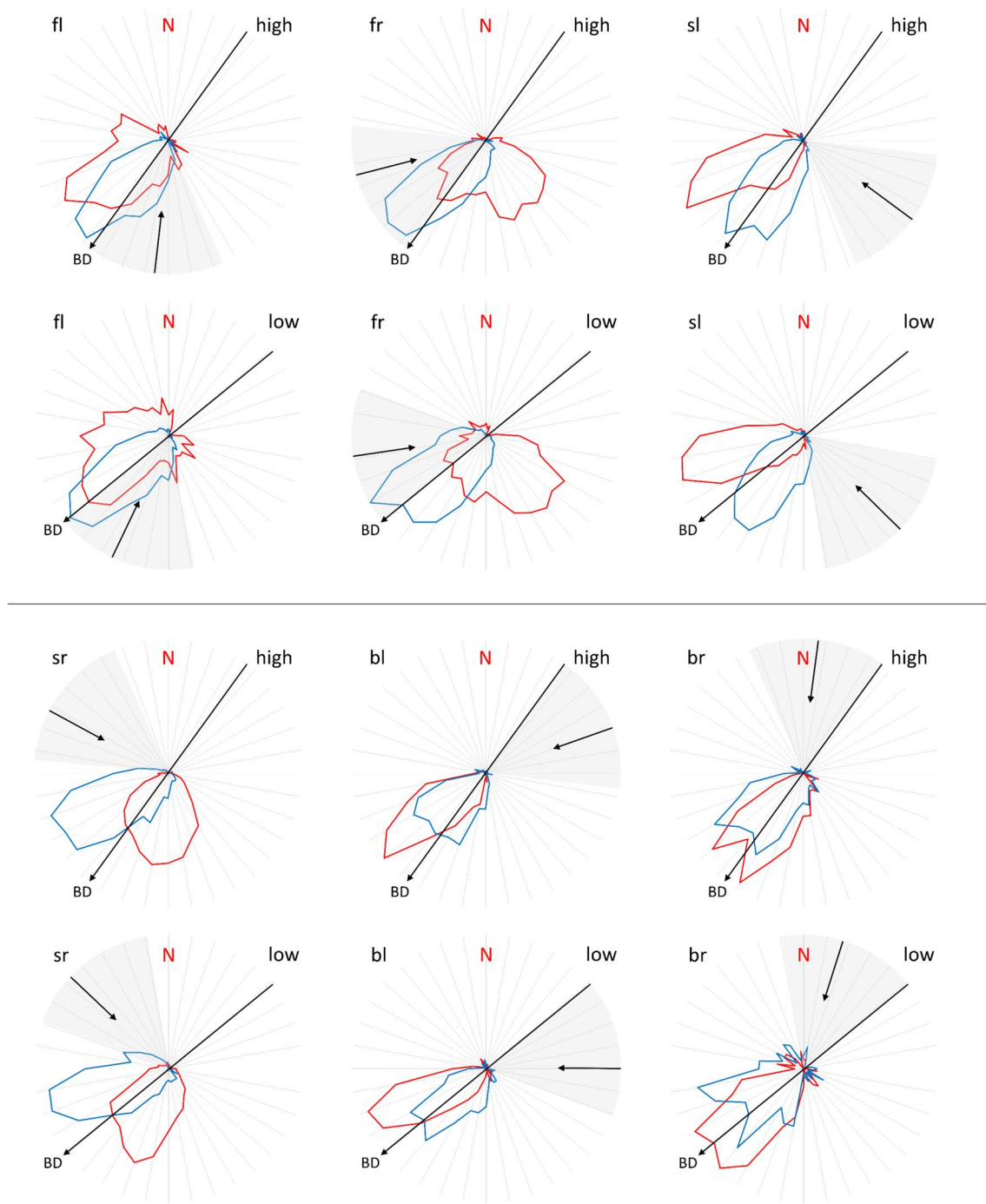


Fig. 7 Circular distributions of tracks (red) and headings (blue) for each of the wind sectors and altitudinal zone presented in Fig. 6. The black arrows through each centre show BD (differing between flight

levels). A black arrow from the periphery towards the centre of the graph indicates the average wind direction per sector (color figure online)

while drift increased with wind speeds above this limit due to lacking or insufficient increase of compensatory efforts. (B) Overcompensation under low wind speeds may be considered as a reaction to tolerated drift under higher wind speeds. (C) With very strong westerly winds, many birds shifted their body axis southward, favouring south- or

south-eastward overdrift. (D) Among the birds with southerly headings under WNW winds, we cannot exclude some pseudo-drift of S-oriented migrants, while active downwind migration (pseudo-drift) towards SE was negligible (except perhaps some birds in early August). (E) Our analysis is not suitable to test Liechti's (1993) conclusion that partial

compensation occurred mainly in relation to wind directions at low flight levels. However, it indicates diminishing scatter of headings around BD in the upper height bin, leading on average to increased drift. This slight increase of drift with altitude would be in line with Liechti's (2006) statement that the effectiveness of visual drift compensation decreases with height above ground.

Our data (Figs. 3b, c and 6) show that winds from $\pm 30^\circ$ around W were by far the most frequent winds, most of them with moderate speeds of 4–12 m/s. Besides these birds battling these opposing winds, the wind sectors fr and sr comprised also the most obvious cases of overcompensation at low wind speeds. Indications of similar behaviour (based on much less data) occurred also in the wind sectors bl and br (i.e. following winds). Within a wind sector the probability is high that the distribution of birds along the axis of wind speeds reflects quantitatively the behaviour of the birds. Thus, a minority of birds flew under weak winds, with an average tendency towards overcompensation in both height bins. Weak following winds can be expected in the eastern half of anticyclones, weak opposing winds along the northern edge of anticyclones. Further studies are needed to learn whether anticyclonic conditions are a precondition for such behaviour.

The comparison of available and used winds (Fig. 3b) reveals that the wind directions in the lower altitudinal zone were used according to availability, except a slight preference for the limited occasions of south-easterly winds. At high flight levels, the scatter of available winds was reduced, and the birds used an even narrower sector of $\pm 20^\circ$ around 280° . A possible explanation of these narrow sectors of available and particularly used winds at altitudes > 1500 m asl may be seen in the reduced influence of topography on wind currents and birds, and in an increasing selection of highly motivated and well-oriented migrants with altitude. The use of wind directions according to availability seems possible because the overall average wind speed was below 5.5 m/s. Considering the distribution of wind speeds (Fig. 3c) reveals, however, a different picture: the strongest winds (from 230° to 280°) were avoided by the migrants. Consequently, the neighbouring sectors to the left and right comprised higher proportions of tracks. Strikingly, the rare winds from sector ENE were relatively strong and overproportionally used by the birds in both height bins. The use of strong westerly winds was generally reduced in comparison with easterly winds. Our very simple comparison of the birds' air speeds with winds from four sectors confirmed an increase of air speeds with opposing and side winds (as predicted by Pennycuick 1972) and slight decrease with following winds at least in high-flying birds. The average air speed (of mainly songbirds) was 11 m/s with negligible winds, thus slightly higher than the theoretical maximum range speed of 10.5 m/s assumed by Liechti (1995) for a

medium-sized passerine. Our data suggest that passerines compensate roughly 10–20% of weak to moderate opposing winds up to about $V_w = 13$ m/s, or up to 14 m/s according to Fig. 4. Observations at an Alpine pass (1950 m asl) differentiated between three size classes of passerines and found that small passerines varied their average air speed between ~ 10 m/s under following winds and ~ 14 m/s under opposing winds (Bloch et al. 1981). Medium-sized passerines varied between ~ 10.6 and ~ 13.6 m/s, while an increase from 12.5 to 13.9 m/s was not significant in large passerines. These findings agree with Pennycuick's (1972) statement that small birds have wider power margins than large ones to adjust their air speed. They do, however, only marginally support the expectation that V_a should decrease with following winds.

A fundamental prediction of the flight aerodynamic theory is that air speed increases with decreasing air density (i.e. with altitude). Accordingly, Bruderer (1971) found an increase of the average air speed by about 10% per kilometre increase in flight altitude above the Swiss Lowlands; Schmaljohann and Liechti (2009) measured 1.0 m/s increase per km height for flap-gliding flyers and 1.4 m/s for (the usually smaller) bounding flyers in the trade-wind zone of the western Sahara. A comparable increase in air speed was not found in the present data set. A possible explanation of this paradox is shown by Fig. 3c: strong winds from WNW and SW were overproportionally used in the lower compared to the upper altitudinal zone. Following winds, on the other hand, were overproportionally used in the upper height bin according to Fig. 3b. This avoidance of opposing winds at high altitude combined with a preference for high flight levels under following winds favours a reduction of average air speed with altitude. Such adjustment of flight altitudes according to wind support was reported e.g. by Bruderer et al. (1995) and Liechti et al. (2000).

Our analysis of individual tracks and allocated winds refines and complements the general conclusions of Alerstam (1976) based on the average movements of multiple echoes on surveillance radar screens: in our data full drift was a most prominent feature under strong winds, the amount of partial compensation decreased with increasing wind speed, and full compensation and even overcompensation occurred at low wind speeds; pseudo-drift was not a relevant part of migration in our area. Observed overdrift was considered as tolerated or supported southward drift. While Alerstam found that birds were extremely rarely overpowered by winds exceeding the birds' air speed, our data indicate that with strong opposing winds deviations of 90° – 180° occurred frequently. Another observed overpowering was retrograde migration in direct headwinds. While Alerstam observed no overcompensation (negative drift), our data comprise frequent overcompensation at very low wind speeds. The warning of Green and Alerstam (2002)

that regressions of individual flight directions in relation to the angle between track and heading of these individuals produce spurious results due to scattering effects of opposing and concentrating effects of following winds was taken into account by considering the effects of winds from six sectors separately.

The high importance of drift in our data stimulates comparison with observations in N America, where some studies even emphasize the occurrence of downwind flights. An important difference between the two sub-continent is that the main mountain ranges in N America run N–S; even the east and west coasts follow this general direction down to the Gulf of Mexico. Between these edges, cyclones can move eastward continuously without major obstructions. Thus, migration might follow simpler rules than in Western Europe. Gauthreaux and Able (1970) concluded and Able (1972, 1973, 1974) repeatedly confirmed that in the south-eastern USA land birds selectively fly with the wind, regardless of its direction or speed, progress of autumn migration being achieved by southward movements reaching on average about five times the intensity of those in other directions. Able (1972) stated that moon-watching observations of Lowery and Newman (1966) are in general agreement with his own data. Our impression is, however, that there are important differences.

Lowery and Newman's impressive illustration of autumn migration in relation to weather and wind systems was based on a continent-wide moon-watch operation with more than 200 observation sites distributed over nearly all states of the USA. The data of four full moon nights (1–5 October 1952) visualized massive southward movements under northerly winds contrasting with reduced migratory intensities under less favourable winds. Weak opposing or side winds did in most cases not prevent the birds from flying southward. Stronger opposing or cross winds led usually to partial drift, rarely to downwind flights. Strong SW to S winds along the Atlantic coast (1–2 October) were associated with birds flying mainly westward away from the coast. Strong NW winds from the Great Lakes towards the Atlantic in the night of 3–4 October led to southward movements between the Lakes and the Atlantic. We conclude that downwind migration occurred mainly with northerly winds, while varying partial compensation was typical for situations with less favourable winds (most impressive the inland movements from the Atlantic coast).

Richardson (1971) visualized three intensity categories of nocturnal spring migration combined with one to three modes of directions per night positioned in a generalized weather map for eastern Canada: with southerly winds on the eastern side of cyclones as well as in the western and central parts of anticyclones strong migration with NE directions prevailed. With easterly winds to the N and northerly winds to the W of low-pressure areas as well in the eastern

parts of anticyclones, the intensity of migration decreased, and directions became scattered (often with one southward mode), thus supporting the idea that fractions of the migratory stream may engage in reverse migration, thus moving with the winds in seasonally inappropriate directions.

Horton et al. (2016) used data of two autumn seasons from three coastal and three inland radar stations and corresponding wind data to calculate the preferred direction of migration (PDM, which varied around SW) and the average distributions of tracks and headings. They concluded that migrants often drifted sideways on crosswinds, but most strongly compensated for drift when near the Atlantic coast; this tendency increased with the progress of the night (as observed by Fortin et al. 1999 along the Mediterranean coasts). We derive from the presented data in Horton et al. (2016) that winds from the left of PDM (i.e. winds from sectors SE and E in autumn) were generally weak and the means of scattered tracks remained around 217° along the coast and around 215° in the inland without notable compensation needed. Winds from the right of PDM (mainly from W to N) were much stronger, resulting in tracks considerably left (S) of PDM and headings right (W) of PDM. Along the coast, compensation was strong (with average headings around 249°, and partially drifted tracks around 195°); inland, headings varied around 228°, tracks around 184°, indicating slightly weaker compensation.

A long-term (1995–2018) surveillance radar study on spring and autumn migration along the Pacific Flyway led the authors (Newcombe et al. 2019) to the statement that overall, spring migrants tended to drift on winds, but less so at northern latitudes and farther inland from the Pacific. According to their Fig. 1 we conclude that spring migrants flying along the Pacific coast had ample possibilities to fly with following winds at all sites N of San Francisco; further S the birds had to cope with unfavourable winds comprising important components from N and W. At all the inland sites the birds were exposed to winds causing partial eastward drift despite a wide scatter of headings indicating compensatory efforts. Similarly during autumn, birds could select times with northerly winds for migration along most of the Pacific coast, while S of Los Angeles winds were widely scattered with eastward and northward components inducing drift increasing with the distance from the coast. Extreme scatter including reverse migration was observed in Nevada (with strong SSW-winds at the SE site and WNW-winds at the NW site). The inland sites in Washington and Oregon showed notable drift due to prevailing westerly winds.

Our conclusion is that the reactions of migrants in N America to winds are not fundamentally different from Europe, but the birds are favoured by frequently occurring supporting winds. Unfavourable winds lead to decreasing migratory intensity, drift, and occasional downwind flights. Intense migration against opposing winds is much less

frequent than in western Europe; accordingly, the occurrence and intensity of migration under such conditions is reduced in N America, but nevertheless possible and partial drift compensation is frequent, particularly in risk-prone areas (e.g. in coastal regions).

Prospects

It will be important to study the reactions of migrating birds to winds in areas with prominent leading lines or barriers, in regions with less variable winds (e.g. in the trade-wind zones), and closer to the birds' destinations, to see how their behaviour is influenced by environmental conditions. Reverse migration merits to be studied in a broader context of meteorological and geographical conditions, as the present data indicate increased occurrence under opposing winds, while Komenda-Zehnder et al. (2002) found no influence of weather factors in the trade-wind zone of southern Israel.

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Author contributions BB designed the project, including the fieldwork and the present analysis; he wrote the article; PK developed and applied the methods for the data analysis, produced most of the graphics, contributed texts for the methods chapter and the figures, and commented on the article; DP selected the required data sets from the radar data bank, prepared some figures, and approved the text.

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Data availability Data and analyses are available at the vogelwarte.ch Open Repository and Archive, <https://doi.org/10.5281/zenodo.14215043>.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights No animals were harmed during the study.

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